FORAGING ECOLOGY OF SHY ALBATROSSES *Thalassarche cauta* BREEDING IN AUSTRALIA: IMPLICATIONS FOR INTERACTIONS WITH LONGLINE FISHERIES

by

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April Hedd

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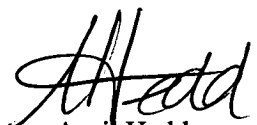

April Hedd 31/ 05/ 99

Shy albatross brooding a chick at Albatross Island, Tasmania.

ABSTRACT

Globally, bycatch associated with longline fisheries poses the most serious threat to albatross populations. Almost half of the populations for which adequate data exist are either currently, or in the recent past they have been in decline, and there is widespread acknowledgment that bycatch in longline fisheries is responsible for these declines. Within the Australian Fishing Zone (AFZ), large numbers of seabirds have been killed in both the Japanese and Australian domestic pelagic longline fisheries targeting Southern bluefin tuna *Thunnus maccoyii*. Attracted to the vessels by baits and offal discharge, seabirds, mainly albatrosses and petrels, ingest baited hooks, become entangled and subsequently drown. Conservative estimates of seabird mortality for the Japanese portion of the fishery indicated that at least 1,000-3,500 birds were killed annually within the AFZ. The Australian domestic longline fishery also has a serious seabird by-catch problem, but the overall mortality rates have yet to be quantified.

Shy albatrosses constitute a significant component of the seabird by-catch in longline fisheries within the AFZ, where an estimated 5,000 individuals have been killed in the Japanese portion of the fishery in the past decade. Shy albatrosses are also the most frequently caught species in the Australian domestic longline fishery. Shy albatrosses *Thalassarche cauta* are endemic to Australia, and they breed in three colonies off the coast of Tasmania; Albatross Island to the north, and Pedra Branca and Mewstone off the south coast. The breeding population size approximates 12,300 pairs annually. Despite the prevalence of this species as bycatch in longline fisheries, their ecology was poorly known. This study, which has examined integrated aspects of both the breeding biology on land and the foraging behaviour at sea, was undertaken to redress the lack of ecological information for the species, and to quantify their degree of overlap with longline fisheries operating within the AFZ.

The foraging ecology was investigated in three main ways; using satellite telemetry to identify the foraging zones at sea; using archival recorders to determine both the diving behaviour and at-sea activity patterns; and by collecting diet samples throughout the chick-rearing period. Parental breeding and provisioning strategies were also investigated using a combination of VHF telemetry and artificial nests which continually recorded chick mass. Patterns of attendance by adults at the colony were also quantified during the breeding and non-breeding periods. All aspects of the foraging ecology and parental provisioning strategies were examined across three breeding seasons to quantify the magnitude of inter-annual variation. Finally, using the full suite of satellite tracking data, an assessment was

made of degree of overlap between the three Shy albatross populations and longline fisheries operating within the AFZ.

Adult Shy albatrosses from all breeding sites in Tasmania foraged locally during the breeding season, being distributed at-sea within 200-300 km of their colonies. Foraging occurred exclusively in neritic waters over the southeast Australian continental shelf, and, at the population level, the foraging locations were highly consistent between years. Despite the spatial proximity of the three colonies, the birds used mutually exclusive foraging zones during the breeding season. While the birds were active at sea during both the day and night, much of their travelling (≈ 80%) was undertaken during daylight hours. Diving formed a significant component of the foraging repertoire of Shy albatrosses. With birds diving to depths of almost 8 m, they substantially exceeded their designation as surface-feeders. Diving occurred exclusively during daylight hours, and as the deepest depths were attained at or near midday, prey capture appeared to be largely visually cued.

The diet of Shy albatrosses was dominated by fish, and to a lesser extent by cephalopods, with tunicates and crustaceans also taken. Jack mackerel *Trachurus declivis*, Redbait *Emmelichthys nitidus*, and Gould's squid *Nototodarus gouldi* were the three most important prey species in all sampling years. These species are common in the shelf region of Tasmania, where they are known to surface school during the day. Information on the behaviour of the birds at sea, coupled with behavioural information on the main prey species combine to indicate that Shy albatrosses have largely predatory foraging habits. Given that the main prey species occur in surface waters during the day, Shy albatrosses could obtain the majority of their food live from surface waters.

Almost year-round attendance at the colony by adults from Albatross Island indicated that the birds likely remained within southeast Australian waters year-round. Unlike any other albatross species studied, Shy albatrosses spend a significant portion of their non-breeding period attending the colony, suggesting that prey remain locally available throughout the year. The provisioning pattern of adults was consistent with short foraging trip durations and neritic foraging habits. Chicks were provisioned at ≈ 400 g/day from the end of the brooding period until fledging, and they were fed at the highest frequency recorded for any albatross species. The flexibility offered by locally abundant prey resources was exemplified during the chick-rearing period. Parents were able to increase provisioning rates when their chicks were hungry, and even faced with nest abandonment by their mates, some single parents were able to successfully raise their chick.

The segregated at-sea distribution of the three Shy albatross populations results in different

likely impacts from fisheries. Given the distribution of effort in longline fisheries within the AFZ and the bird's consistent foraging locations between years, it is likely that birds breeding at Pedra Branca and Mewstone suffer substantially from overlap with longline fisheries. However, seemingly during both the breeding and non-breeding periods adult birds from Albatross Island remain relative remote from fishing operations. The unknown status of the populations at Pedra Branca and Mewstone, along with the little known distribution of juveniles, is therefore of considerable concern. Future research on Shy albatrosses must endeavor to identify the foraging grounds of non-breeding birds (both adults and juveniles), and determine the demographic parameters and status for the three populations.

This study has examined a number of aspects of the foraging ecology of the Shy albatrosses, elevating the species from one of the least known (Croxall 1998) to one of the better understood. It is clear that only armed with a through understanding of albatross ecology coupled with widespread adoption of appropriate and effective mitigation measures, that we can begin securing a future for albatrosses and succeed in ensuring their long-term survival.

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I have been fortune enough during this project to have spent extended periods of time on Albatross Island. While I thank everyone who has helped out with the fieldwork, I am particularly grateful to a number of people. A special thank-you first to Nigel Brothers, for sharing with me his wealth of knowledge and understand of Shy albatrosses, and also for the many times he's gone in the field to deploy and retrieve gear from the albatrosses. Many thanks also to Doozie both for accompanying Nigel on many of these trips, and for his help many times on Albatross Island. To Jenny Scott and Al Wiltshire for both their similar love of albatrosses and special places like Albatross Island and their unending enthusiasm. Thanks also to Neil Smith for transport to and from the Islands, and for his constant smile.

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Chapter 1

GENERAL INTRODUCTION

1.1 BACKGROUND

Members of the Family Diomedeidae, the albatrosses, are characterized by a delayed onset of maturity, low reproductive output, slow post-natal development and naturally high rates of adult and juvenile survival. With such extreme life-history characteristics, populations and even species are vulnerable to threats that reduce either the annual survival rates of adults or recruitment of juveniles into the breeding population.

Today, by-catch associated with longline fisheries is the most serious and pervasive threat facing albatrosses globally (Gales 1993 & 1998, Croxall 1998), and the extent of such mortality is widely acknowledged as responsible for widespread declines in the size of albatross populations worldwide (Alexander et al. 1997, Gales 1993 & 1998, Gales et al. 1998). Indeed, over half of the albatross populations for which adequate data exist are either currently, or in the recent past they have been, in decline (Gales 1993 & 1998). Large numbers of seabirds are killed within the Australian Fishing Zone (AFZ) each year as a result of incidental capture in both the Japanese and Australian domestic pelagic longline fisheries targeting Southern bluefin tuna *Thunnus maccoyii* (Brothers 1991, Brothers & Foster in press, Gales et al. 1998).

Pelagic longline fishing involves deployment of a single mainline to which a series of baited hooks are attached via branch lines. The Japanese fleet operates vessels that range between 45 and 60 m in length and from a 100 km mainline they set between 2,400 and 3,000 barbed steel hooks per day. The lines take approximately five hours to set and during the process, a bait is cast once every six seconds. Smaller vessels (18-45 m) operate in the Australian domestic longline fleet, and they set 20 to 40 km long lines that each contain 600 to 1,500 hooks. Birds are attracted to the vessels both by the baits and by discharged offal. Baits are available for scavenging by the birds until they sink out of their reach in the water column ($\geq$ 10 m). After ingesting the baited hooks they become entangled, are subsequently hauled under the water and drowned. The extent of longline mortality suffered by an albatross population is largely dictated by the magnitude and duration of fishing activities that occur within their foraging zones.

Japanese longline fishing has occurred in Australian waters since the 1950's, but effort peaked early in the 1990's when over 30% of their global longlining effort (21 million hooks) occurred within Australian waters. Japanese effort has since contracted, and following an inability to ratify the Trilateral Agreement (Australia, Japan and New Zealand) for 1998 tuna quotas, the Japanese have been denied access to fish within the AFZ. The Australian domestic longline fishery commenced in the 1980's and effort has increased annually since then, exceeding 7 million hooks by 1997 (Gales et al. in press). Estimates of seabird by-catch rates in the Japanese portion of the fishery have been calculated largely from data collected and carcasses retained through the Australian Fisheries Management Authority (AFMA) fisheries observer program. As seabird data is collected incidentally to fish data, and given that 30% of the birds caught are never hauled aboard (Brothers 1991), resulting estimates of seabird by-catch rates must be considered as absolute minimums. By-catch rates in this fishery were estimated in the order of 0.15 birds/1000 hooks between 1988 and 1995 (Gales et al. 1998), resulting in minimum mortalities of 1,000-3,500 birds per year. Shy albatrosses constituted a significant proportion of the seabird by-catch in this fishery, with 5,000 birds (*Thalassarche cauta* plus *T. steadi*, in unknown proportions) estimated to have been killed within the AFZ alone in the past decade (Gales et al. 1998). Shy albatrosses are also the most frequently caught species in the Australian domestic longline fishery (Tasmanian Parks & Wildlife Service, unpubl. data), and while this fishery is also known to have a serious seabird by-catch problem (Brothers & Foster in press) overall by-catch rates have not yet been quantified.

Despite the prevalence of Shy albatrosses *Thalassarche cauta* as a by-catch species, and both their Australian and global designation as *Vulnerable* (Croxall & Gales 1998), Croxall (1998) noted that Shy albatrosses were one of the least-known of all albatrosses. Published accounts of the ecology of the species in Australia were restricted to a single collection of diet samples by Green (1974), and a description by Johnstone et al. (1975) of the population size and breeding behaviour of birds at Albatross Island. There was little information regarding aspects of the species breeding biology, their distribution or behaviour at sea, and little quantitative information on the diet. To redress this inadequacy, a detailed study examining integrated aspects of the breeding and foraging ecology of this species was undertaken.

1.2 SPECIES AND STUDY SITES

Shy albatrosses are endemic to Australia (Nunn et al. 1996, Robertson & Nunn 1998),

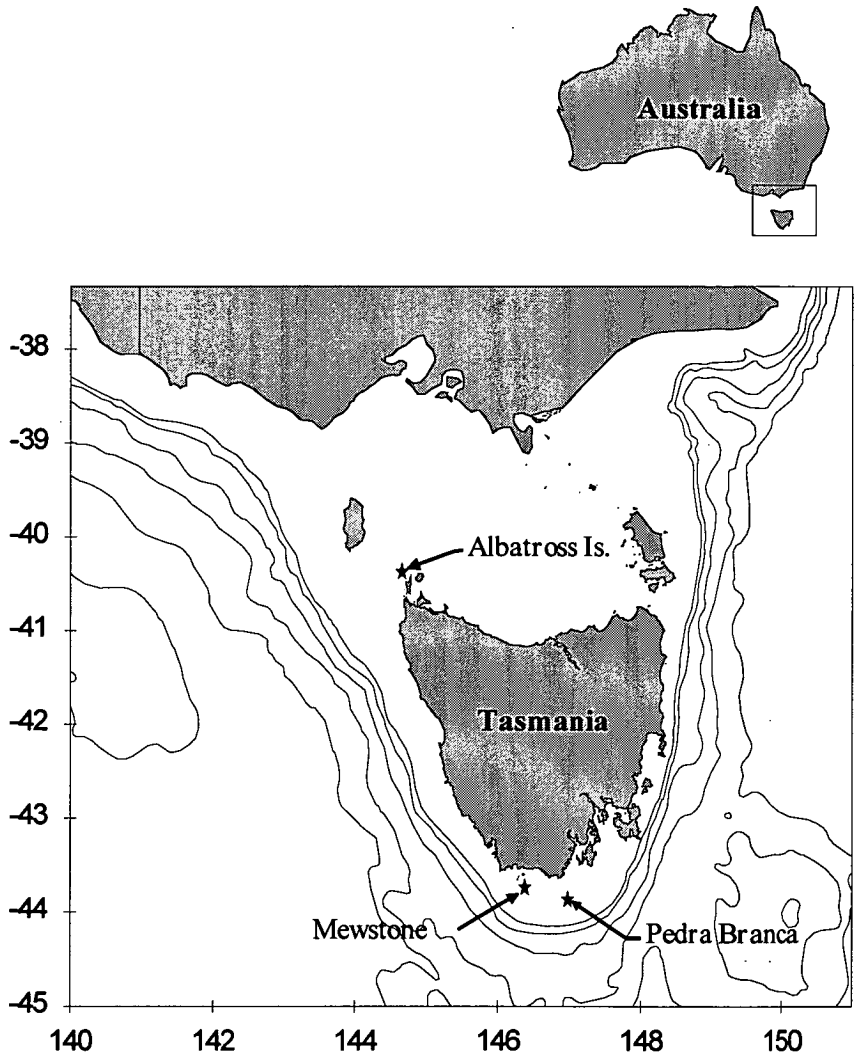

Figure 1.1: Map showing the location of Shy albatross breeding sites in Tasmania.

and the species breeds in three colonies off Tasmania; Albatross Island (40.375° S, 144.656° E) to the northwest, with 5,000 breeding pairs per year, and Pedra Branca (43.867° S, 146.967° E) and Mewstone (43.742° S, 146.375° E) off the south coast, where approximately 250 and 7,000 pairs breed each year (Gales 1998, Figure 1.1). The total breeding population size therefore approximates 12,250 pairs.

While medium sized amongst albatrosses (3.0-5.0 kg), Shy albatrosses are the largest of the *Thalassarche* group. Breeding occurs annually, commencing when the birds are 5 years of age (N. Brothers, unpubl. data). Egg-laying begins late August and extends until October, but most eggs are laid in September. After an incubation period of approximately 70 days, the single chick hatches in early December and is brooded in alternate shifts by both parents over the next 3-4 weeks. Chicks are left alone at the nest late December/early January after which time adults forage simultaneously, yet independently, for food for themselves and their single chick. Chicks fledge in April, after spending approximately 18 weeks on the nest, and they remain absent from the natal colony for at least the next two years (N. Brothers, unpubl. data).

Estimates of the population size are of moderate accuracy only, except at Albatross Island, where counts are conducted annually (Gales 1998). A long-term monitoring program was established at Albatross Island early in the 1980's (by N. Brothers), and ground counts of the breeding population size and chick banding have been conducted annually since this time. The population at Albatross Island is slowly recovering from the devastation executed by feather hunters and egg collectors at the turn of the Century. While numbers have increased from only 300 pairs in 1909 to 5,000 pairs currently, this represents just 25% of the original population estimate (Gales 1998, N. Brothers unpubl. data). The rate of recovery of this population is slowed by incidental mortality of both adults and juveniles in longline fisheries. The status of the populations at Pedra Branca and Mewstone is unclear. This is of concern given that the sedentary nature of adults and the distribution of longlining effort within the AFZ indicates that it is likely these populations that are most seriously impacted by local longline fishing.

1.3 AIMS OF THE PROJECT

The broad aim of this project was to examine the ecology of Shy albatrosses, integrating aspects of both the breeding biology on land and the foraging behaviour at sea. The study was conducted over three breeding seasons, and across the three breeding localities, although work was focused at Albatross Island. Working over three consecutive breeding

seasons allowed quantification of the nature and magnitude of inter-annual variation, and ultimately enabled assessment of risks posed by fisheries operating within the AFZ.

The study had the following objectives:

1) to quantify aspects of the species foraging ecology by:

   - identifying the foraging locations using satellite telemetry; conducting both inter- and intra-annual comparisons of foraging zone use;
   - investigating both the diving capabilities of the birds and their behaviour at-sea using archival data loggers;
   - quantifying the composition of the diet during the chick-rearing period, and documenting any inter-annual variation;

2) to examine the parental investment and breeding strategies of adults by:

   - monitoring annual patterns of adult attendance at two of the breeding sites;
   - documenting the chick provisioning and growth strategies throughout the rearing period;

3) to determine the level of interaction of the birds with fishing operations by:

   - determining for each population the degree of overlap with Japanese and Australian domestic longline fisheries within the AFZ;
   - estimating the proportion of the diet originating as discards from fishing operations.

1.4 ORGANIZATION OF THE THESIS

This thesis comprises two sections. Section A (Chapters 2 to 4) covers methodological and preliminary studies. As techniques were required to determine the sex of adult and fledging-aged Shy albatrosses in the field, morphometric indices for externally sexing the birds were developed and presented in Chapter 2. Chapters 3 and 4 provide preliminary assessments of both the foraging zones and diving behaviour of adult Shy albatrosses in Tasmania. Chapter 3 details the foraging movements of birds from Albatross Island and Pedra Branca during a single breeding and post-breeding period. Chapter 4 describes the diving behaviour of Shy albatrosses using both maximum depth gauges and archival time-depth recorders. Experimentally derived estimates of the accuracy of both techniques, within the depth range exploited by the albatrosses, are also discussed. While I conducted the experimental trials presented in Chapter 4, field collection of the data

presented in both this and Chapter 3, was carried out by my Supervisor, Rosemary Gales and her colleagues. As this work provided the foundation for much of the subsequent research, and as it remained largely unanalyzed when this project began, we felt that its analysis and incorporation into the thesis was an important precursor to undertaking the remainder of the work.

Section B provides a series of four Chapters that describe the ecology of Shy albatrosses. Chapter 5 details the year-round colony attendance patterns of the albatrosses at both Albatross Island (1995/96 to 1997/98) and Pedra Branca (1997/98), while Chapter 6 details the composition of the diet during the chick-rearing period at Albatross Island. In this Chapter information relating both to the behaviour of the albatrosses at sea and the behaviour and biology of their main prey were integrated to elucidate the nature of Shy albatross foraging behaviour. Chapter 7 describes both the provisioning strategies of adults and the growth rates of chicks between hatching and fledging. As data were collected at Albatross Island over three breeding seasons, variation was assessed both within and between years. Chapter 8 provides an integrated picture of the foraging distribution, foraging strategy, and at-sea segregation of the three populations. Implications of the differential distributions in terms of interactions with fisheries were also separately assessed for each population.

In the General Discussion (Chapter 9) the major attributes which combine to reveal the uniqueness of Shy albatrosses within the Diomedeidae are synthesized and described. A precis of the major threats facing this endemic species, along with recommendations for future research priorities, are also provided.

With the exception of the General Introduction (Chapter 1) and the General Discussion (Chapter 9), all Chapters are self-contained and have been written as papers. This results in some repetition of information, especially within the Methods sections. Chapters 2 to 4 have already been published and details of the Journals are given at the start of each Chapter. With the exception of some minor formatting changes, these papers have been presented as published, however, their Abstracts and Reference lists have been removed and incorporated into the general Abstract and Reference list for the thesis, for consistency.

Section A

Methodological and Preliminary Studies

Chapter 2

RELIABILITY OF MORPHOMETRIC MEASURES FOR DETERMINING THE SEX OF ADULT AND FLEDGLING SHY ABLATROSSES, *Diomedea cauta cauta*, IN AUSTRALIA

April Hedd, Rosemary Gales & Nigel Brothers

2.1 INTRODUCTION

Procellariiformes generally exhibit sexual dimorphism where males are larger and heavier than females, but the degree of overlap renders sexing without behavioural or morphometric confirmation questionable. Consequently, unless observed during copulation or recently following egg-laying, albatrosses and petrels are difficult to sex in the field. This uncertainty can hinder ecological investigations, as in some species the division of duties during incubation and brooding (Black-browed albatross *Diomedea melanophris* Tickell & Pinder 1975, Wandering albatross *Diomedea exulans* Croxall & Ricketts 1983, Antarctic petrel *Thalassoica antarctica* Lorentsen & Rϕv 1995), the foraging locations (Wandering albatross, Prince et al. 1992, Weimerskirch et al. 1993), and the diet (Giant petrels *Macronectes spp.* Hunter 1984, Wandering albatross, J.P. Croxall unpubl. data, cited in Croxall 1995) have been shown to differ between the sexes. Division of duties at the nest may also differ with overall body size and the corresponding ability to withstand extended fasting periods (Croxall & Ricketts 1983; Warham 1990), and disparate foraging zones and prey items may reduce intraspecific competition for food resources.

Within albatrosses, Wandering and Royal *Diomedea epomophora* show the greatest degree of sexual dimorphism in weight, with males approximately 20% larger than females (Croxall 1982b). These species can also be sexed on plumage differences when pairs are observed together, as females are generally the darker of the two (Warham 1990). The smaller albatrosses, however, show less marked dimorphism in size and no sex difference in plumage characteristics.

Shy albatrosses are medium sized albatrosses with breeding populations generally confined to the Australian and New Zealand regions. Results of a major taxonomic revision of albatrosses recommended adoption of nomenclature in which Australian Shy albatross populations comprise a distinct species (Nunn et al. 1996, Robertson & Nunn in

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press). This species breeds in three colonies off Tasmania and occurs or disperses over the Australian continental shelf and slope waters year round (Marchant & Higgins 1990, Reid et al. in press).

As part of an ongoing study into the ecology of this species, it was necessary to investigate the possibility of sexing individuals using morphometric parameters which can be reliably and rapidly measured on live birds (i.e., measures of the head and beak). Dissection and measurement of carcasses provided data from known-sex birds from fledgling-age through to adulthood. Adult carcasses were obtained from birds killed on longlines set off Tasmania, while fledgling-aged carcasses were obtained from birds typically dying from an avian pox viral infection at the Albatross Island colony off northern Tasmania. Sex determination was required to examine possible sex-related differences in provisioning strategies as well as any sex differences in the foraging zones of adults and juveniles.

2.2 METHODS

In Australia, Shy albatrosses breed in three colonies off Tasmania; Albatross Island (40° 23' S, 144° 39' E) in western Bass Strait, Pedra Branca (43° 52' S, 146° 58' E) and the Mewstone (43° 45' S, 146° 23' E) south of the State. The earliest age at first breeding is 5 years, eggs are laid in September, chicks hatch in December and fledge during April (N Brothers, unpubl. data).

The sex of 97 fledgling-aged Shy albatrosses (approximately four months of age; 52 males, 45 females) from Albatross Island was determined by dissection between 09-14 April 1996. Only freshly dead fledglings with no remaining down were included in the sample. The seemingly large number of dead chicks resulted from an avian pox virus which, in some years, is responsible for the death of large numbers of fledgling-aged birds at the Albatross Island colony. Coupled with the rapid onset of the disease, the favourable condition of these chicks, as evidenced from extensive interstitial fat reserves and high body mass, made it likely that growth to fledgling-age was unimpaired. These chicks can therefore be expected to satisfactorily represent their cohort.

Adult and sub-adult Shy albatrosses which were retained frozen after being killed on longline hooks within the Australian Fishing Zone were also examined. Age classes were distinguished based upon relative beak colour: the tips of the upper and lower mandibles of fully mature birds are pale yellow, while sub-adult birds retain darkness at the bill tips

until they reach five to seven years of age (N Brothers, unpubl. data). Sub-adults were classed as birds beyond their first year which still retained a degree of darkness in the upper and/or lower mandibles. Forty-two birds (13 males and 29 females), frozen shortly after death, were sexed by dissection and a suite of external measurements were taken.

The following beak, head and leg measurements (in mm) were taken from the adult and sub-adult birds using vernier calipers (± 0.1 mm): culmen length (CL), upper bill depth (UBD), minimum bill depth (MBD), basal bill depth (BBD), bill width (BW), head with (HW), head length (HL);(Figure 2.1), tarsus length, length of the middle-toe, and claw length on the middle toe. Tail length and the following wing measurements were also taken with a tape rule (± 1 mm): wingspan, full wing length, length of the humerous, and wing length from the carpal joint to the tip of the outer primaries. For one sub-adult female the middle-toe claw was broken and for two adult and one sub-adult female damage to the tail feathers prevented measuring tail length. Measures of the head and beak, along with the weight of fledgling-aged birds was also taken. Fledglings were weighed using a 10 kg Salter spring balance (± 50 g), stomachs were extracted, and the quantity of food within the stomach was subtracted from the total weight prior to analysis. As unknown quantities of water were incorporated into the carcasses of the adult and sub-adult birds as a result of drowning, it was not possible to obtain an accurate weight. For this reason, weights are not reported for these birds. Damage to the bill made it impossible to measure BW for one male and two female fledglings, and for another of the female fledglings BBD and HW could also not be measured.

As previous studies (e.g., Barrett et al. 1989) have identified significant inter-observer variability in morphometric measures, and given that morphological differences are used not only to sex birds, but also to elucidate their provenance away from the breeding colony, we investigated the extent of experienced observer variability when measuring Shy albatrosses. Thirty-seven of the 42 adult and sub-adult birds were independently measured by three observers for this analysis, and the variability in each measure was assessed using a repeated measures analysis of variance. As Observer 1 (N.B.) held the most experience in measuring seabirds, his measurements were used to calculate the adult/sub-adult discriminant function analysis. Fledgling-aged birds were measured either by Observer 3 (A.H) or by a fourth observer (R.G), who also has extensive experience with seabirds. The seven head and beak measures indicated in Figure 2.1 comprised input to separate Stepwise Discriminant Function Analyses (DFA, Statistica version 4.5, StatSoft, Inc.) for sexing both adult/sub-adult and fledgling-aged birds. This

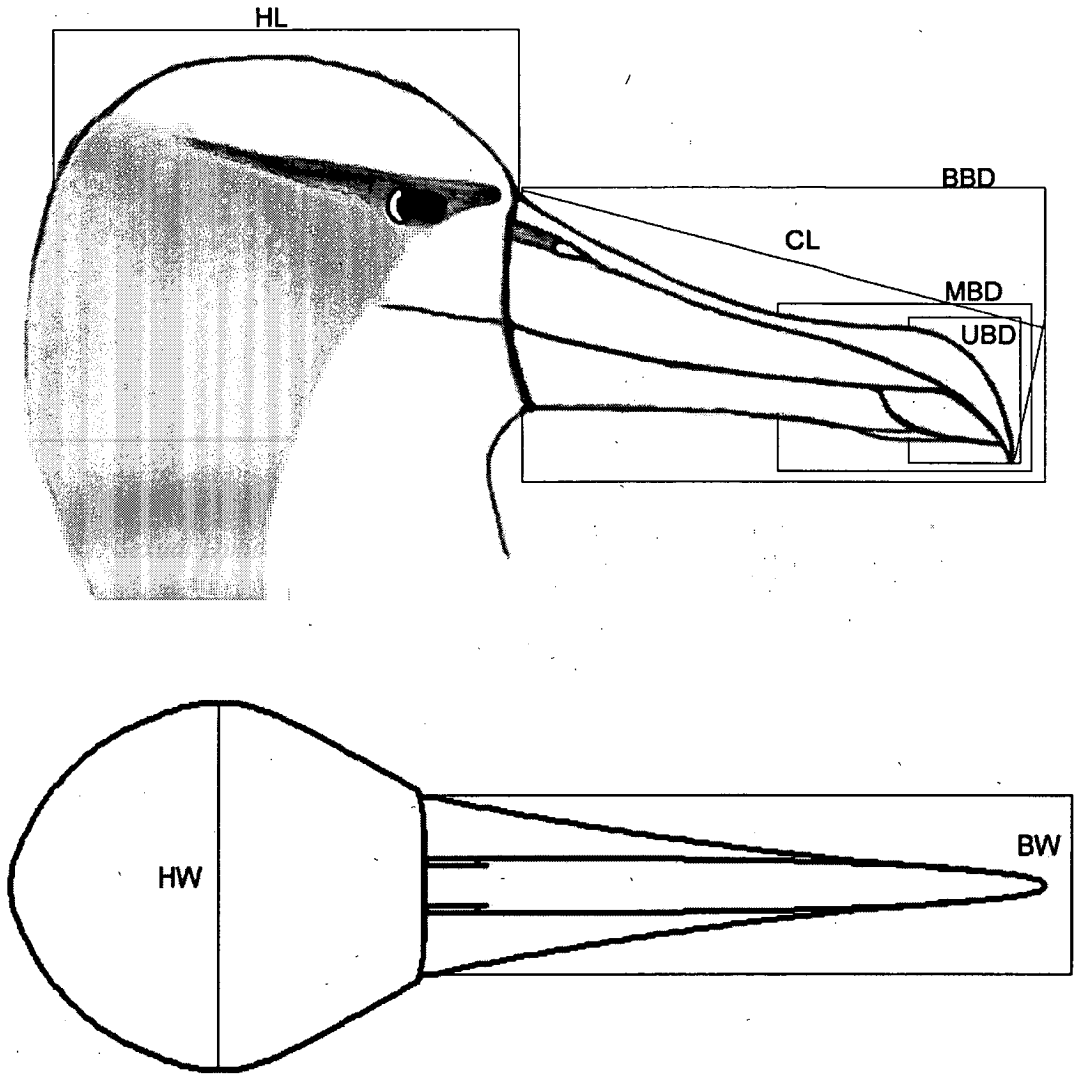

Figure 2.1: Schematic Shy albatross depicting head and bill measurements (HL = head length, HW = head width, BW = basal bill width, CL = culmen length, BBD = basal bill depth, MBD = minimum bill depth, UBD = upper bill depth).

approach builds a model to determine group membership using only variables which contribute most to group discrimination. The power of the resulting adult/sub-adult DFA was cross validated by running beak and head measurements from previously unsexed breeding pairs through the equation. These pairs were observed at their nest sites, and each individual tentatively identified as male or female based upon relative within pair size. The power of the DFA was assessed by determining the percentage allocation of each member of the pair to a different sex. As the adult/sub-adult DFA identified all but one of the fledgling-aged birds as female, separate DFAs were run for the adult/sub-adult and fledgling-aged birds.

Canonical loadings, which indicate the strength of the relationship between the parameter and group discrimination, are also presented. These values vary from -1 to +1, with larger canonical loadings indicating increasing discriminatory power. Univariate statistics (one-way ANOVAs) determined whether single morphometric parameters differed between the sexes both within and between age classes. In addition, an index of dimorphism was calculated for each measure (mean female character/mean male character x 100). All morphometric measures were tested for and exhibited normality (Komolgorov-Smirnov, $p > 0.05$), and an alpha level of 0.05 was adopted to indicate statistical significance.

2.3 RESULTS

2.3.1 *Adult and sub-adult birds*

Descriptive statistics for all external measurements and the index of sexual dimorphism for adult (n=27) and sub-adult (n=15) Shy albatrosses are shown in Table 2.1. Adult and sub-adult birds were indistinguishable in all measurements (one-way ANOVAs, $p > 0.05$ for all comparisons), and, as a result, the data were pooled; they will be hereafter referred to as the adult/sub-adult group of birds. Males were significantly larger than females in all measures of the head, beak and leg, while the sexes were similar in measures of the tail and wings (Table 2.1). Although there was considerable overlap between the sexes, UBD and HW were the most dimorphic features, indicated by their relatively large F ratios (Table 2.1).

A DFA incorporating the seven head and beak measurements yielded a success rate of 98%, with 41 of the 42 birds being correctly sexed. The single error resulted from a relatively small male being classified as a female. A stepwise DFA also yielded a 98%

Table 2.1: Morphometric measurements (mm) and index of sexual dimorphism for adult and sub-adult Shy albatrosses. The first two parameters (UBD and HW) are those required by the discriminant function analysis to correctly sex the birds 98% of the time.

Parameter	Sex	n	Mean	SD	Range	Dimorphism index	F-ratio	p level
Upper bill depth (UBD)	Male	13	34.0	0.95	32.2 - 35.6	94.4	49.86	< 0.001
	Female	29	32.1	0.73	30.1 - 33.4			
Head width (HW)	Male	13	71.1	1.53	68.5 - 74.0	94.9	47.99	< 0.001
	Female	29	67.5	1.54	64.1 - 70.0			
Culmen length (CL)	Male	13	137.8	3.95	130.9 – 146.5	96.4	19.29	< 0.001
	Female	29	132.8	3.21	125.8 – 138.0			
Minimum bill Depth (MBD)	Male	13	30.6	1.17	28.9 - 32.4	95.4	23.09	< 0.001
	Female	29	29.2	0.73	28.1 - 30.5			
Basal bill depth (BBD)	Male	13	54.7	2.00	51.6 - 58.1	95.2	22.07	< 0.001
	Female	29	52.1	1.45	48.8 - 55.0			
Basal bill width (BW)	Male	13	34.8	1.31	31.7 - 36.5	94.8	23.15	< 0.001
	Female	29	33.0	0.98	31.5 - 35.2			
Head length (HL)	Male	13	85.4	4.97	74.7 - 96.6	96.0	7.83	0.008
	Female	29	82.0	2.90	77.0 - 87.0			
Tarsus length	Male	13	91.1	3.03	84.4 - 95.6	97.3	7.27	0.010
	Female	29	88.6	2.63	82.6 - 94.9			
Length of middle-toe	Male	13	122.1	3.74	115.0 - 128.3	95.6	22.59	< 0.001
	Female	29	116.7	3.25	111.0 - 122.6			
Claw length on middle-toe	Male	13	20.1	1.53	17.6 - 22.5	91.5	11.06	0.002
	Female	28	18.4	1.50	15.0 - 20.0			
Tail length	Male	13	223.5	10.51	200 - 239	96.7	1.05	> 0.05
	Female	26	216.2	9.63	201 - 237			
Wingspan	Male	13	2,370	126.7	2,175 - 2,678	98.9	0.58	> 0.05
	Female	29	2,343	96.5	2,160 - 2,545			
Wing length	Male	13	1,180	65.4	1,098 - 1,353	97.6	1.72	> 0.05
	Female	29	1,152	62.0	1,080 - 1,320			
Humerous length	Male	13	592	42.5	552 - 720	98.8	0.23	> 0.05
	Female	29	585	42.5	540 - 696			
Wing length from carpal joint to tip of longest primary	Male	13	348	32.1	317 - 448	99.1	0.08	> 0.05
	Female	29	345	35.7	314 - 440			

success rate using just UBD and HW, with the same male being misclassified. The following discriminant equation resulted:

$$D = 3.17\ (\text{UBD}) + 1.61\ (\text{HW}) - 217.58$$

A negative discriminant score indicates that a bird is female, while a positive score indicates a male. The canonical loadings of these parameters were relatively high: 0.688 for UBD and 0.675 for HW. When tested on a sample of 20 previously unsexed birds (10 pairs), this equation sexed the smaller member of the pair as female and the larger as male in 18 out of 20 cases (90% of the birds). The errors resulted when both members of a pair were assigned to the same sex. In the first instance, when both birds were classified as females, the correctly sexed bird had a discriminant score of -8.7, clearly a female, while the score for its mate was -1.7, indicating that it was a relatively small male. The second error resulted when both birds were classified as males. The correctly sexed individual here had a discriminant score of +7.1, while its mates score was +0.5 Discriminant scores of the dissected birds differed significantly with sex (Table 2.2), and their distribution was markedly different (Figure 2.2A).

Table 2.2: Sexual dimorphism in the discriminant scores of adult (UBD and HW) and fledgling (MBD, HW and HL) Shy albatrosses.

Age class	Sex	Mean ± SD (n)	Range	F-ratio	p level
Adults	male	4.5 ± 3.67 (13)	-1.9 - 12.5	105.2	< 0.001
	female	-6.3 ± 2.90 (29)	-14.1 - -0.6		
Fledglings	male	2.9 ± 2.23 (52)	-3.0 - 7.9	124.8	< 0.001
	female	-2.3 ± 2.36 (44)	-6.0 - 5.1		

2.3.2 *Inter-observer differences in morphometric measures*

With the exception of MBD, BW, HL and the length of the claw on the middle-toe, significant inter-observer differences existed in all other morphometric measures (Table 2.3). Nevertheless, measures of the head, bill and legs were quite similar between observer, and generally varied by less than 1.0 mm. Inter-observer differences were much greater in the wing measurements, with both means and standard deviations being

Table 2.3: Means and standard deviations for each morphometric measure of Shy albatrosses made by three different observers. Repeated measures analyses of variance tested for observer differences in each parameter, and post-hoc tests were conducted using Tukey's HSD procedure.

Parameter	Observer 1 Mean ± s.d.	Observer 2 Mean ± s.d.	Observer 3 Mean ± s.d.	F- ratio	p- level	Post-hoc test
CL	134.3 ± 4.04	133.3 ± 4.06	133.5 ± 4.04	37.8	< 0.001	1 ≠ 2,3
UBD	32.7± 1.05	32.5 ± 1.02	33.0 ± 1.10	15.9	< 0.001	1 ≠ 2 ≠ 3
MBD	29.6 ± 1.02	29.8 ± 1.12	29.5 ± 0.95	3.1	> 0.05	
BBD	52.8 ± 1.92	54.9 ± 2.52	54.9 ± 2.53	44.8	< 0.001	1 ≠ 2,3
BW	33.6 ± 1.34	33.8 ± 1.38	33.9 ± 1.49	2.8	> 0.05	
HW	68.7 ± 2.19	68.6 ± 2.11	68.2 ± 2.31	3.3	< 0.05	1 ≠ 3
HL	83.2 ± 3.75	83.5 ± 3.00	83.3 ± 3.91	0.3	> 0.05	
Tarsus	89.6 ± 2.79	90.8 ± 3.23	91.6 ± 2.96	16.7	< 0.001	1 ≠ 2,3
Middle toe	118.6 ± 4.22	118.3 ± 3.88	119.2 ± 4.69	3.6	< 0.05	2 ≠ 3
Claw length on middle toe	19.0 ± 1.67	19.0 ± 1.52	19.1 ± 1.63	0.3	> 0.05	
Tail length	219.1 ± 10.34	220.3 ± 7.11	222.0 ± 7.55	3.4	< 0.05	1 ≠ 3
Wingspan	2,357 ± 110.3	2,507 ± 80.7	2,520 ± 80.3	101.2	< 0.001	1 ≠ 2,3
Wing length	1164 ± 65.8	1248 ± 43.3	1241 ± 41.9	82.8	< 0.001	1 ≠ 2,3
Humerous length	348 ± 35.8	427 ± 11.2	430 ± 10.4	210.3	< 0.001	1 ≠ 2,3
Wing length from carpal joint to tip of longest primary	589 ± 44.0	674 ± 16.9	681 ± 18.2	194.2	< 0.001	1 ≠ 2,3
Birds assigned to the correct sex (%)	97.6	89.2	91.9			

highly variable (Table 2.3).

When Observer 2 and Observer 3's measures were run through the discriminant function equation (developed from Observer 1's measures), more sex allocation errors were found, with 89 and 92% of birds correctly assigned to sex, compared with 98% achieved for Observer 1.

2.3.3 *Fledgling-aged birds*

The weight, beak and head measurements and the index of sexual dimorphism for all morphometric measures of the fledglings are given in Table 2.4. Male fledglings were heavier and larger than females in all measures, although again the sexes overlapped considerably. The most dimorphic features for fledgling-aged birds were in the measures of bill depth (UBD, MBD, and BBD) and the head dimensions (HL and HW; Table 2.4).

In this case the DFA incorporating all seven measures correctly classified 89% of the fledglings to the correct sex, with 10% (five) of males and 12% (five) of females being misclassified. Using a stepwise DFA, 88% of the fledglings were correctly classified using just MBD, HW and HL. In this case, four (8%) small males were classed as females and eight (18%) large females were classed as males. Although more females than males were misclassified, the result was not statistically significant ($\chi^2 = 1.33$, df = 1, $p > 0.05$). The following discriminant function was obtained:

$$D = 1.26\,(\text{MBD}) + 0.4\,(\text{HW}) + 0.57\,(\text{HL}) - 105.93$$

Again, a negative discriminant score indicates a female, and a positive result a male. The canonical loadings for these parameters were again high: 0.706 for MBD, 0.569 for HW, and 0.599 for HL, and one could expect to correctly classify the sex of 88% of fledgling aged birds by restricting measurements to these three parameters. The discriminant scores again differed according to sex (Table 2.2), although the range was more restricted and the overlap more extensive than for adults/sub-adults (Figure 2.2B).

2.3.4 *Changes in morphometric parameters with age*

Running morphometric parameters for fledgling-aged birds through the adult/sub-adult DFA resulted in 96 of the 97 birds being classified as female. This error rate (53%) necessitated the development of an age-specific discriminant function equation for sexing this species. In all morphometric measurements fledglings of both sexes were

Table 2.4: Morphometric measurements (mm), weight (g) and index of sexual dimorphism for fledgling-aged Shy albatrosses. The first three parameters (MBD, HW and HL) are those required by the discriminant function analysis to correctly sex fledglings 88% of the time.

Parameter	Sex	n	Mean	SD	Range	Dimorphism index	F-ratio	p level
Minimum bill depth (MBD)	Male	52	27.9	1.08	24.7 - 30.2	93.5	64.95	< 0.001
	Female	45	26.1	1.15	22.9 - 28.5			
Head width (HW)	Male	52	67.6	3.02	56.8 - 78.4	95.0	42.62	< 0.001
	Female	44	64.2	1.77	59.6 - 68.3			
Head length (HL)	Male	52	81.8	2.27	75.0 - 88.1	96.6	43.83	< 0.001
	Female	45	79.0	1.91	74.8 - 83.8			
Culmen length (CL)	Male	52	130.2	4.26	120.4 - 143.2	97.2	19.71	< 0.001
	Female	45	126.6	3.58	119.8 - 137.5			
Upper bill depth(UBD)	Male	52	29.2	0.97	26.6 - 31.9	95.5	48.58	< 0.001
	Female	45	27.9	0.99	25.9 - 30.9			
Basal bill depth (BBD)	Male	52	51.5	1.86	48.1 - 57.3	95.0	50.69	< 0.001
	Female	44	48.9	1.63	45.3 - 52.5			
Basal bill width (BW)	Male	51	32.7	1.28	30.0 - 36.8	96.0	21.28	< 0.001
	Female	43	31.4	1.54	29.0 - 37.0			
Mass (g)	Male	52	3842	498.5	2,550 – 5,250	92.2	11.20	0.001
	female	45	3542	363.7	2,550 – 4,200			

significantly smaller than corresponding measures for the adults/sub-adults (Table 2.4; one-way ANOVAs, $p<0.001$ for all parameters). Depending on the parameter examined, female fledglings ranged from 86.8-96.3% of adult/sub-adult female size, and male fledglings similarly ranged from 85.9-95.8% of adult/sub-adult male size (Table 2.5).

Trends were similar between the sexes, with the greatest differences between adult/sub-adult and fledgling-aged birds being in measures of bill depth and bill width.

The greater separation of adult/sub-adult discriminant scores indicates that they can be sexed more reliably than fledgling-aged birds from external measurements (Figure 2.2).

Table 2.5: Analyses of variance testing for changes in each morphometric parameter with age for both sexes. The percentage of adult size attained by the fledgling-aged birds for each measure is also given.

Parameter	Males			Females		
	F-ratio	p level	Adult size attained (%)	F-ratio	p level	Adult size attained (%)
CL	34.1	< 0.001	94.5	56.0	< 0.001	95.6
UBD	255.0	< 0.001	85.9	409.5	< 0.001	86.8
MBD	64.1	< 0.001	91.1	168.6	< 0.001	89.6
BBD	29.8	< 0.001	94.1	72.9	< 0.001	93.9
BW	27.4	< 0.001	94.0	26.7	< 0.001	95.2
HL	14.8	< 0.001	95.8	28.8	< 0.001	96.3
HW	15.8	< 0.001	95.1	66.0	< 0.001	95.1

2.4 DISCUSSION

Like most other Procellariiformes studied, both adult/sub-adult and fledgling aged Shy albatrosses show sexual dimorphism in a number of morphometric measures with males generally being larger than females. Adults and sub-adults, however, can be sexed more reliably than fledglings. By taking a single bill measurement (the upper bill depth) and the head width of an adult/sub-adult Shy albatross and calculating a simple discriminant score, 98% of birds can be correctly sexed. The comparable value is 88% for fledgling-aged birds by taking an alternative bill measurement (the minimum bill depth) together with the head length and width.

While the adult/sub-adult DFA delivers a 98% success rate, sex allocation errors will still

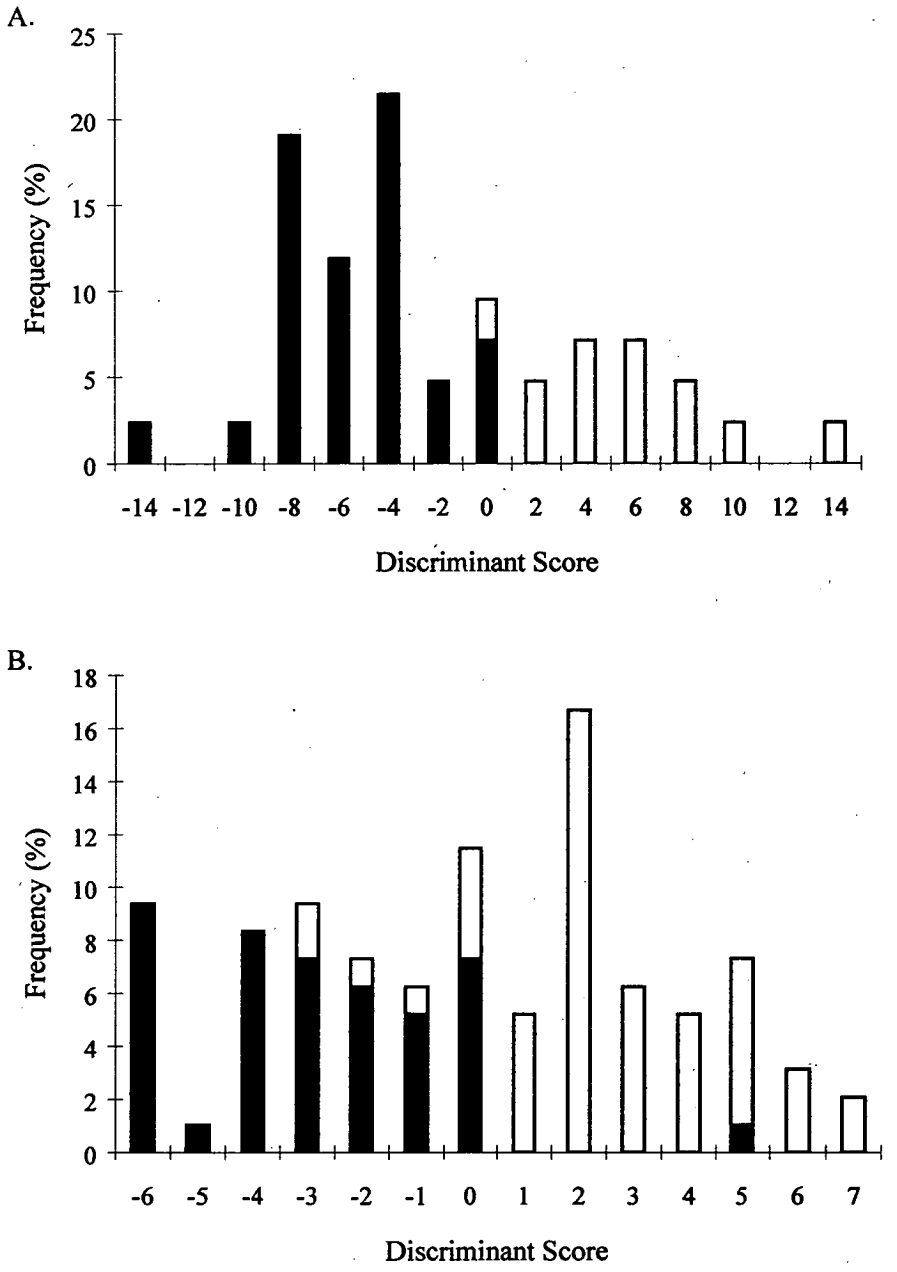

Figure 2.2: Distribution of discriminant scores for (A) sub-adult/adult and (B) fledgling-aged Shy albatrosses whose sex was determined by dissection (□ = males, ■ = females).

result when discriminant scores fall within the overlap zone. Similar to the two breeding pairs in this study where both individuals were assigned to the same sex, such errors could be avoided or at least minimized when working with breeding birds by measuring both members of the pair. Inspection and comparison of the resulting discriminant scores would enable correct assignment of sex.

Sexual dimorphism in body weight of Procellariiformes was summarized by Croxall (1982b). While sex differences in the body weight of the black-backed albatrosses generally do not exceed 10%, the Waved albatross is an exception with males almost 20% heavier than females. Fledgling-aged Shy albatrosses in this study were typical of the group, with males being approximately 8% larger than females. Weight differences alone, however, can be misleading (see Croxall's 1995 comments on Fairbairn & Shine 1993) as they change both throughout the breeding season (Prince et al. 1981; Croxall 1995) as well as with age (Brooke 1978, Prince et al. 1981, Weimerskirch 1992). Measuring head and beak parameters which do not show such variation would provide more reliable results.

The extent of adult/sub-adult sexual dimorphism in morphometric measures found for Shy albatrosses (91.5-99.1%) is comparable to values calculated from data contained in the Handbook of Australian New Zealand and Antarctic Birds (HANZAB, Marchant and Higgins 1990) for other black-backed or 'mollymawk' albatrosses (Grey-headed *Diomedea chrysostoma*, Black-browed, and Bullers *Diomedea bulleri*). Comparable values range from 92.6% for the minimum bill depth of Black-browed albatrosses from South Georgia to 101.0% for tarsus measures of Buller's albatrosses from New Zealand. Although sample sizes and the range of mollymawk species for which comparable data are available are rather small, it appears that bill depth and width, along with the width of the head (taken in this study) may be among the most dimorphic of the standard seabird measures for this group. Comparing Shy albatrosses to the Great albatrosses, again using data from HANZAB (with sample sizes for each sex being at least five individuals), dimorphism indices were again similar, with values ranging from 89.4% for the basal bill depth of Wandering albatrosses from Antipodes Island, to 100.2% for the wing length of Royal albatrosses *Diomedea epomophora sanfordi* from Chatham Island. Dimorphism indices for Sooty albatrosses *Phoebetria fusca* are also similar, being greater than 90% for all measures (Berruti 1979).

Few data exist on size differences between fledgling-aged and adult albatrosses. The

only directly comparable data are for fledgling-aged Sooty albatrosses where culmen lengths are 94.4% of adult size (Berruti 1979). This compares well with this study, where culmen lengths of Shy albatross fledglings averaged 95.1% of adult/sub-adult size. Other measures from fledgling-aged Sooty albatrosses indicate that birds range from 90.5-97.7% of adult size when they fledge. Shy albatrosses also fledge before attaining adult/sub-adult morphometric proportions. The similarity in size between sub-adult and adult birds could indicate that growth is substantially complete by the end of the first year. But, as most of the sub-adult birds were unbanded, the age at which asymptotic size is reached is unknown.

The percentage of adult/sub-adult Shy albatrosses which can be correctly sexed using the discriminant function analysis is higher than for many other petrel species (Croxall 1982b, Sagar 1986, Genevois & Bretagnolle 1995), while the success rate for sexing the fledglings (88%) is similar to other work examining dimorphism in this age class. Scolaro (1987), for example, indicated that 93.1% of Magellanic penguin *Spheniscus magellanicus* fledglings could be correctly sexed using only two external measurements.

While there was significant inter-observer variability in most morphometric measures, those of the wings and tail showed the highest degree of variability, and those of the head and beak showed the least. The high variability in wing and tail measurements, even on a sample of dead birds, would seem to make them less appropriate than head and beak measures for either sexing or assigning provenance to a given bird. Differences in observer methodology can lead to significant variation in morphometric measures, and these differences must be considered when comparing samples of birds both within and between studies. Even with such difference, however, analyses indicated that for Shy albatrosses in Tasmanian colonies, any experienced observer could correctly assign sex to approximately 90% of adult/sub-adult birds by using the DFA derived in this study.

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Chapter 3

FORAGING MOVEMENTS OF THE SHY ALBATROSS *Diomedea cauta cauta* BREEDING IN AUSTRALIA: IMPLICATIONS FOR INTERACTIONS WITH LONGLINE FISHERIES.

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3.1 INTRODUCTION

The global decline in numbers of many albatross populations has inextricably been linked to interactions with longline fisheries, as birds striking at baited hooks set to catch fish become hooked or entangled and drown (Weimerskirch & Jouventin 1987, Croxall et al. 1990, Brothers 1991, Vaske 1991, Gales 1993, Murray et al. 1993, de la Mare & Kerry 1994, Prince et al. 1994, Croxall et al. in press, Gales in press, Prince et al. in press, Weimerskirch & Jouventin in press). Tens of thousands of albatrosses die annually in the Japanese portion of the Southern Bluefin Tuna *Thunnus maccoyii* fishery each year (Brothers 1991).

The influence of longline fisheries on demographic trends in albatrosses is most thoroughly documented for Wandering Albatrosses *Diomedea exulans* breeding on South Georgia in the South Atlantic, and on Crozet and Kerguelen Islands in the Indian Ocean (Croxall et al. in press, Weimerskirch in press, Weimerskirch et al. 1997). Following dramatic declines in the 1960s and 1970s, Wandering Albatross numbers in the Indian Ocean have increased since the mid-1980's, coincident with decreased longline fishing within their foraging zones (Weimerskirch & Jouventin in press, Weimerskirch et al. 1997). The outlook for Wandering Albatrosses breeding on South Georgia is bleak. Again, coincident with intensive longline fishing in their foraging zones, Wandering Albatross from South Georgia have steadily declined since the mid-1970's (Croxall et al. 1990 & in press, Prince et al. in press). The positive demographic status of Wandering Albatrosses on Crozet and Kerguelen Island has coincided with the shift of Japanese Southern Blue-fin Tuna longline vessels outside the foraging zones of these birds during the breeding season. Any potentially favourable effects for Wandering Albatrosses breeding on South Georgia have been countered by the development of longline fisheries for Patagonian Toothfish *Dissostichus eleginoides* close to their breeding grounds (Croxall et al. in press). Although demographic information is less extensive for the

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smaller *Diomedea* and *Phoebetria* albatrosses, numbers in both the Indian Ocean and the South Atlantic continue to decline (Prince et al. 1994, Croxall et al. in press, Weimerskirch in press, Weimerskirch et al. 1997). Longline associated mortality both in and outside the breeding season has contributed to these declines (Croxall et al. in press, Weimerskirch & Jouventin in press).

Results of a major taxonomic revision of albatrosses recommended adoption of nonmeclature in which the Australian Shy Albatrosses comprise a distinct species (Nunn et al. 1996, Robertson & Nunn in press). This species breeds in three colonies off Tasmania and remains in large numbers over the Australian continental shelf and slope waters throughout the year (Marchant & Higgins 1990, Reid et al. in press). While the overall abundance of the birds indicates the presence of New Zealand Shy Albatrosses, ringing recoveries and colour marking studies indicate that Tasmanian birds are relatively sedentary after reaching maturity (Brothers et al. in press).

The sedentary nature of the species is cause for concern, given the seasonal shift and spatial concentration of Japanese longline fishing within the Australian Fishing Zone (AFZ, Caton et al. 1995) combined with a concomitant increase in the Australian domestic longlining effort (Caton et al. 1995, Brothers & Foster in press). In 1990, over 20 million longline hooks were set by Japanese and Australian vessels targeting Southern Blue-fin Tuna within the AFZ. Although Japanese effort has fluctuated between 10 and 21 million hooks set annually since 1990, the Australian domestic effort has increased three-fold, from 695,000 hooks in 1991 to 2.1 million hooks in 1994 (Australian Fishing Management Authority, unpubl. data). This represents a proportionate increase from 3 to 10% in the total Japanese effort within the Zone. Between 400 and 1,500 Shy Albatrosses are estimated to die annually on Japanese longline hooks set within the AFZ (Klaer & Polacheck 1995). While it is suspected that a number of these birds are from New Zealand, any mortality is substantial given that the total breeding population in Australia is estimated at 13,000 pairs (Brothers in Gales in press). While each year the Japanese fishery is increasingly concentrating its efforts in winter, the Australian domestic fleet fishes year-round in inshore waters (Caton et al. 1995), thus heightening their potential for contact with this shelf-feeding species (Marchant & Higgins 1990, Reid et al. in press). Shy Albatrosses are killed in the Australian domestic longline fishery (Brothers & Foster in press), but the annual kill rate is yet to be quantified.

As vulnerability to longline fishing may differ between foraging zones used by albatrosses (Weimerskirch et al. 1986, 1988, Weimerskirch in press), it is necessary as a first step towards determining these differences to identify the foraging zones actually

used by birds at different sites. To assess relative vulnerability to fisheries, the spatial and temporal overlap between Shy Albatrosses breeding both north and south of Tasmania with the Japanese longline fishery was analysed. Analyses were limited to overlap with Japanese vessels as comparable data for the Australian domestic fleet was not available.

3.2 METHODS

3.2.1 *Species and Study Sites*

Shy Albatrosses are medium-sized (3.5-5.0 kg), sexually dimorphic albatrosses (Hedd et al. 1998 and Chapter 2), with breeding colonies generally confined to Australian and New Zealand regions. In Australia, Shy Albatrosses breed on three islands off Tasmania: 5,000 pairs on Albatross Island (40° 23' S, 144° 39' E) in western Bass Strait, and 250 pairs on Pedra Branca (43° 52' S, 146° 58' E) and 7,000 pairs on the Mewstone (43° 45' S, 146° 23' E), both south of Tasmania. The albatrosses breed annually at these sites, beginning when the birds are 5 years of age. Most eggs are laid in September, and the single chick hatches in December. The brood/guard period lasts approximately three weeks, after which both parents feed the chick for a further 14-16 weeks; fledging typically occurs during April (N. Brothers, unpubl. data). The general routes of post-fledging dispersal appear to be specific to the natal colony, with juveniles from Albatross Island heading west and travelling as far as Western Australia, while those from the Mewstone traverse both the Indian and Pacific Oceans, moving into waters off South Africa and New Zealand (Brothers et al. in press). Immature birds begin returning to the colonies when two to three years old (N Brothers, unpubl. data).

3.2.2 *Field Protocol*

The field studies were carried out at Albatross Island and Pedra Branca. Breeding birds from Albatross Island were satellite tracked during the periods of early incubation (September 1993), brooding (December 1993 and 1994) and late chick-rearing (April-May 1994). Birds from Pedra Branca were tracked during late incubation and early chick brooding in December 1994, and during late chick-rearing (March-April) in 1995. Both Telonics ST10 Platform Terminal Transmitters (PTTs; 85 g, 9.0 cm x 4.2 cm x 1.7 cm; representing 1.9-2.4% of adult body mass) and Toyocom 2038C PTTs (120 g, 13.0 cm x 3.5 cm x 1.8 cm; 2.6-3.4% body mass) were used at both colonies. All PTTs ran continuously and transmitted signals every 90 seconds. Battery life was about one month.

Prior to deployment of PTTs, their operation and accuracy was determined by running them from the field sites for a minimum of 24 hours. Once operation was confirmed, the PTTs were attached directly to the central back feathers using TESA® tape. They were deployed on 44 unsexed breeding birds, and information on foraging location was collected subsequently during 66 trips to sea. The data set includes one bird tracked during both incubation and brooding in 1993, and 14 birds that were tracked for two or more successive trips during late incubation or brooding in 1993 or 1994. Stainless steel rings were placed on the left leg and colour markings on the breast so that birds could be identified quickly when they returned to the colony. Foraging trip duration was determined from satellite transmission reports augmented by repeated attendance checks at colonies, made at a maximum of two hours apart. Observations at colonies were often carried on continuously during daylight to obtain as precise departure and arrival times as possible for the transmitter-bearing birds.

3.2.3 *Data Management*

Location of birds at sea were obtained from the ARGOS system (Toulouse, France). ARGOS location files were initially run through Wildlife Computers SATPAK30 Software version 3.0 (Redmond, Washington, USA), which consolidates locations from the ARGOS Systems Diagnostic and Dispose files in a single file. The data were then filtered with an adapted version of the iterative forward, backward velocity averaging filter of McConnell et al. (1992). The maximum travelling speed of Shy Albatrosses calculated from locations with an accuracy of ≤ 1 km (ARGOS Class 1-3 locations) was 27.8 km/h Locations with a velocity greater than the estimated maximum mean travelling speed (30 km/h) were rejected. Subsequently, 102 locations (7% of the at-sea data; or 6% of the total data set) were discarded.

As the filtering routine operates on running mean of the travelling speed, the first two and last two locations of any file are unfiltered; a minimum of five locations are therefore required to "filter" a single location. Because of this requirement, 20 at-sea locations were arbitrarily chosen as a minimum requirement for application of the filter (27% of foraging trips). For trips with less data, locations between which the rate of travel exceeded 30 km/h were discarded manually. Thirty-eight locations (10% of the at-sea data; 2% of the total) were removed.

3.2.4 *Home range analyses*

Fixed Kernel home range analyses (with the smoothing factor chosen via least squares cross-validation; Worton 1989) were computed using RANGES V Software (R. Kenward, Institute of Terrestrial Ecology, Wareham, Dorset, UK), and used to identify and compare (via Overlap Analysis) the sectors of the ocean (the foraging zones) used by birds during different breeding stages. The asymptote of the home range area (the number of locations beyond which the size of the home range did not increase) was calculated at 50 locations for breeding birds and 20 locations for post-breeding birds. As the number of at-sea locations for individual breeding birds was small, data for individuals within a particular breeding stage and site were pooled. Analyses were further limited to the first foraging trip of an individual to ensure statistical independence in the data. The larger number of at-sea locations for post-breeders allowed estimates of the foraging zone for each individual. Examination of utilisation plots revealed that the area incorporating 95% of the locations (the 95% isopleth) adequately described the core foraging zones of the albatrosses.

3.2.5 *Flight Patterns and Winds*

Flight patterns were interpreted with respect to wind direction and speed from data collected within a 6 h window and from successive locations separated by a maximum of 4.5 h (see Results - constitutes "Group B"). Such restrictions minimized errors in general bearing and distance travelled that resulted from zigzagging flight or intermittent periods of flying and resting upon the water. Chi-square analyses were used to test whether the bird's flight path was random in relation to wind direction and speed. Birds were considered to be flying with the wind when the heading of the bird relative to the wind was between 0 and 60°, with side winds when this angle was between 61 and 120°, and against the wind when it was between 121 and 180° (Weimerskirch & Robertson 1994). Information on wind speed and direction (10 m above sea level) was obtained (Bureau of Meteorology in Hobart) every 3 h from a series of automatic recording stations along the Tasmanian or southeast Australian coastline. Wind information was extracted from the recording station closest to the bird throughout its foraging trip.

3.2.6 *Interaction with Fisheries*

The foraging locations of the birds were analysed for potential overlap with Japanese Southern Blue-fin Tuna vessels in the AFZ. Fishing effort was defined as the number of hooks set in 1° x 1° grid squares between 39-46° S and 137-154° E (areas used by Shy Albatrosses) concurrent with collection of satellite tracking data. Data relating to

Japanese fishing effort were provided by the Australian Fisheries Management Authority (AFMA).

The distance travelled on a foraging trip refers to the total distance covered by a bird from the time it departs the breeding colony until its subsequent return, while the foraging range was defined as the straight line distance from the breeding colony to the satellite location received furthest afield.

Statistical analyses were performed using SYSTAT for Windows version 5.03 (Evansdale, Il, USA). Analyses of variance and Tukey's HSD's tested for differences in foraging trip characteristics between different breeding stages, and data are reported as means ± 1 S.D. as appropriate.

3.3 RESULTS

3.3.1 *Effect of Breeding Stage on the Recovery of Devices*

All PTTs from birds tracked early in the breeding season (incubation and brooding) were recovered. However, during late chick rearing (mid-April 1994 on Albatross Island with chicks approximately one week from fledging, n=4, and mid-March 1995 on Pedra Branca with chicks approximately 5-6 weeks from fledging, n=3), only one of eight devices was recovered; all other birds prematurely deserted their chicks. In April 1994, the partner of just one of the transmitter-bearing birds continued to feed its chick, suggesting that the provisioning period was nearing an end. Although probably hastened by disturbance, the resulting tracks represent movements during post-breeding dispersal, when adults vacate the colonies for 6-12 weeks (Chapter 5). In April 1994, three of the four chicks fledged, while the fate of the fourth chick is unknown. Despite being deployed three weeks earlier in March of the next year, all instrumented birds (n=3) again failed to return to the colony over the next 25 days. Here, partners continued to provision the chicks at an average interval of 3.0 ± 2.0 days (n=5). Although the fate of these chicks is unknown, they appeared healthy upon our departure from the island some three weeks after PTTs were attached to their parents.

3.3.2 *Rate of Travel*

An average of 5.6 ± 2.8 satellite-signalled locations were received per PTT per day (n=327 complete tracking days) for a total of 1711 locations. The accuracy's of these

locations, assessed from running the PTTs from an established location, are given in Table 3.1. In some instances, individual location accuracy was considerably less than that stated by ARGOS, but, on average, the accuracy for class 1-3 locations was similar. The probability of receiving a location signal (determined by the satellite pass distribution at a given latitude) was not equal across a 24 h period; the majority of locations were received between 0300-0900 h and 1600-2200 h local time (GMT + 10 h; Figure 3.1A). This clustering explained an apparent relationship between the distance travelled by the birds and their travelling speed, suggesting that birds either moved slowly (Group A) or relatively quickly (Group B) over a given distance. Figure 3.1B emphasizes the disparity between Group A and B movements with data collected from Albatross Island during September and October 1993. This "relationship", however, was found to be simply an artefact of the data, driven by the time elapsing between successive location signals. Where allocation to "group" was unclear (travelling speeds of less than 5 km/h *and* movements of less than 15 km), locations were removed from these analyses. Locations from "Group A" (those apparently spanning the gap in satellite passes) were separated by 9.4 ± 6.6 h (range 2.2-61.3 h, n=404) while "Group B" locations were separated by 1.8 ± 0.7 h (range 0.0-4.5 h, n=582; two sample t-test, $t_{984}=27.6$, $p < 0.001$; Figure 3.1C). Less frequent locations resulted in lower apparent flight speeds, as they fail to detect both subtle movements and changes in direction, a finding similarly described by Walker et al. (1995).

3.3.3 *Changes in Foraging Range throughout the Breeding Season*

When incubating or rearing small chicks, Shy Albatrosses from both colonies fed relatively locally, either over the continental shelf or the shelf break, never crossing into oceanic pelagic waters (Figure 3.2).

To ensure statistical independence, only the first foraging trip of an individual was used to calculate descriptive statistics for the successive breeding stages. In terms of both the distances covered and the length of time spent at sea, this trip was found similar to subsequent trips (one-way ANOVA, $F_{1,33}=1.3$, $p \geq 0.05$, $F_{1,33}=0.7$, $p > 0.05$, respectively). distribution for the time elapsed between successive Group A and Group B locations (n=986).

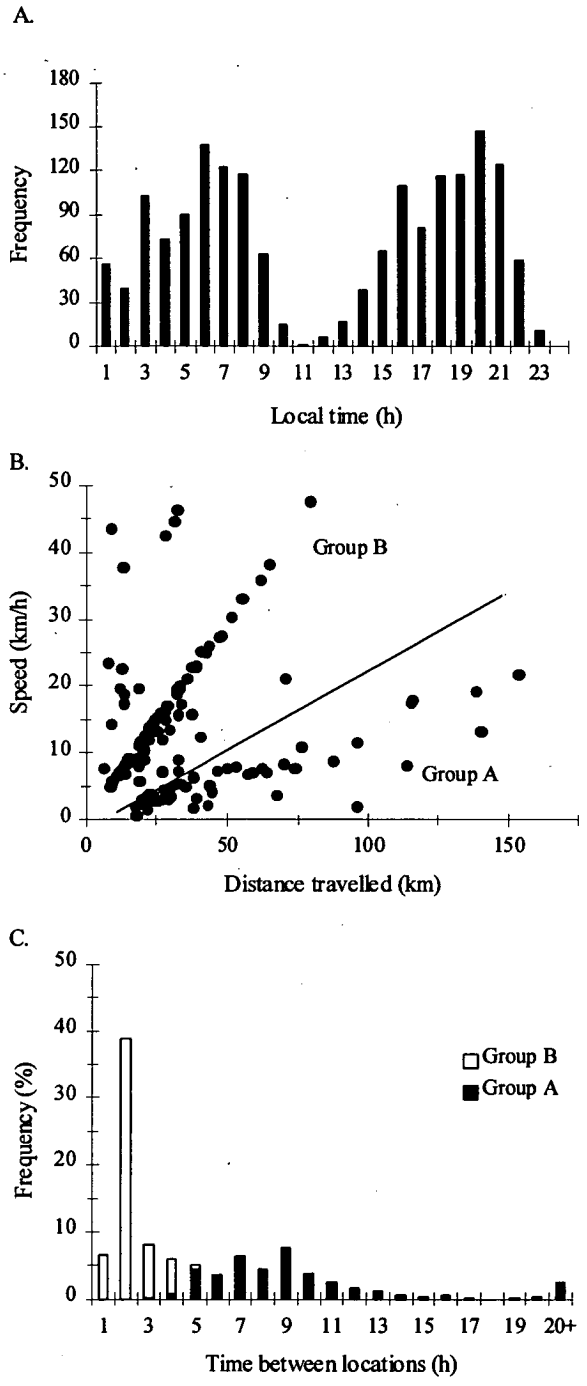

Figure 3.1: Characteristics of the ARGOS locations: (A) Frequency distribution of the local time of locations (n=1,711), (B) Relationship between distance travelled and travelling speed, for Group A and Group B data collected between September and October 1993 (n=161); the line separates locations in Groups A and B, and (C) Frequency distribution for the time elapsed between successive Group A and Group B locations (n=986)..

Table 3.1: Errors in the accuracy of PTTs used on Shy Albatrosses (assessed from fixed location tests) between September 1993 and March 1995. Prior to June 1994 information on ARGOS location accuracy (within one standard deviation) was provided in four Classes (Class 3=150m; Class 2=350m; Class 1=1km; Class 0 accuracy to be determined by the user). Since then 3 additional Classes of accuracy have been added (A, B and Z whose accuracy is unspecified) and Class 0 is now defined as accurate "above" 1km.

Class	n	Latitude error (km) ± s.d	Range (km)	Longitude error (km) ± s.d.	Range (km)
3	27	0.3 ± 0.3	0.0 - 1.1	0.2 ± 0.2	0.0 - 0.9
2	34	0.4 ± 0.7	0.1 - 3.2	0.7 ± 1.0	0.0 - 4.3
1	73	0.6 ± 2.0	0.0 - 2.8	0.8 ± 1.4	0.0 - 5.6
0	62	2.9 ± 4.1	0.0 - 18.01	6.3 ± 13.1	0.0 - 60.3
A	20	5.0 ± 8.6	0.1 - 33.1	4.8 ± 6.2	0.2 - 20.4
B	10	10.2 ± 10.7	0.4 - 29.0	13.2 ± 14.9	1.5 - 50.3
Z	1	0.11	-	0.17	-

Successive trips for a given individual were obtained only during the brooding phase, when birds spend 1-2 days at sea. The paucity of locations received on these trips (7 ± 6, n=34) made it impossible to determine whether birds revisited the same areas during subsequent trips. Due to small sample sizes for some stages and breeding sites (Table 3.2), statistical comparisons of trip characteristics were limited to early incubation and brooding from Albatross Island in 1993, and late incubation from Pedra Branca in 1994. Duration of foraging trips, maximum foraging range and the distance travelled varied with breeding stage (Table 3.2; one-way ANOVAs, $F_{2,31}=25.5$, $p < 0.001$, $F_{2,31}=22.6$, $p < 0.001$ and $F_{2,31}=17.9$, $p < 0.001$, respectively). Birds travelled further, ranged wider and spent longer periods at sea during early incubation than either late incubation or brooding (Tukey's HSD, $p < 0.05$ for all comparisons). Movements during late incubation and brooding were similar in all measures (Tukey's HSD, $p > 0.05$ for all). The maximum foraging range of any breeding bird was 265 km from its colony.

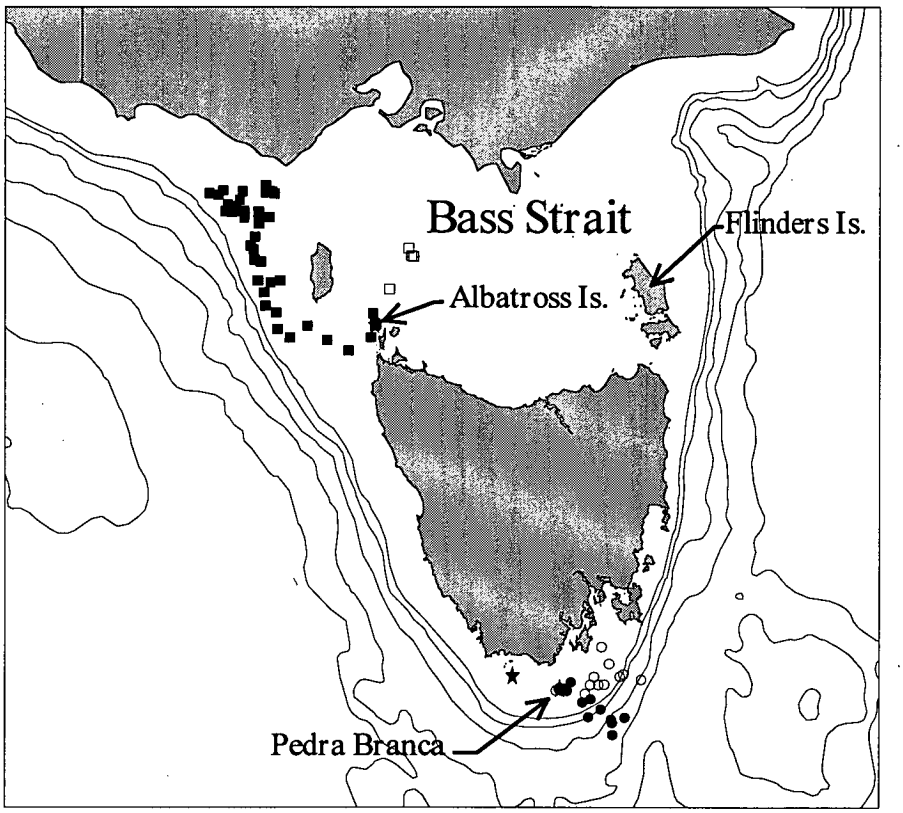

Figure 3.2: Recorded foraging tracks of birds from Albatross Island during early incubation (■) and brooding (□) in September and December 1993, respectively, and from Pedra Branca during late incubation (●) and brooding (○) in December 1994.

Table 3.2. Distance covered, foraging range and duration of Shy Albatross foraging trips during successive breeding stages (mean ± s.d., range and sample size). Only the first trip for an individual is included.

Period and location	n	Distance travelled (km)	Foraging range (km)	Trip duration (days)
Early incubation	8	720 ± 350	197 ± 46	4.6 ± 1.8
September 1993		325 - 1412	141 - 265	2.0 - 6.9
(Albatross Island)				
Late incubation	5	377 ± 244	93 ± 23	2.4 ± 1.6
December 1994		193 - 787	69 - 118	1.0 - 4.1
(Pedra Branca)				
Chick brooding	21	208 ± 106	90 ± 39	1.3 ± 0.5
December 1993		47 - 408	24 - 144	0.5 - 2.4
(Albatross Island)				
Chick brooding	2	198 ± 8	99 ± 1	1.6 ± 0.4
December 1994		192 - 203	98 - 100	1.3 - 1.8
(Albatross Island)				
Chick brooding	1	150	72	1.9
December 1994				
(Pedra Branca)				
Chick rearing	1	377	58	2.4
April 1994				
(Albatross Island)				

The time that breeding birds spent at sea was significantly related to both the distance they covered (r^2=0.85, $p < 0.001$) and their maximum foraging range (r^2=0.62, $p < 0.001$; Figure 3.3).

Post-breeding birds from both colonies remained in the coastal waters off southeast Australia, but, overall, ranged further than breeders ($F_{1,42}$= 67.2, $p < 0.001$, Table 3.3). The mean maximum foraging range of post-breeding birds from Albatross Island was 308 ± 125 km (n=4), and from Pedra Branca 501 ± 163 km (n=3). The furthest movement recorded by this study was one post-breeder, who moved 673 km from its breeding colony.

3.3.4 *Foraging Zones determined from Home Range Analyses*

3.3.4.1 Breeding birds:

Data for individuals were pooled to estimate the foraging zones of breeding birds from

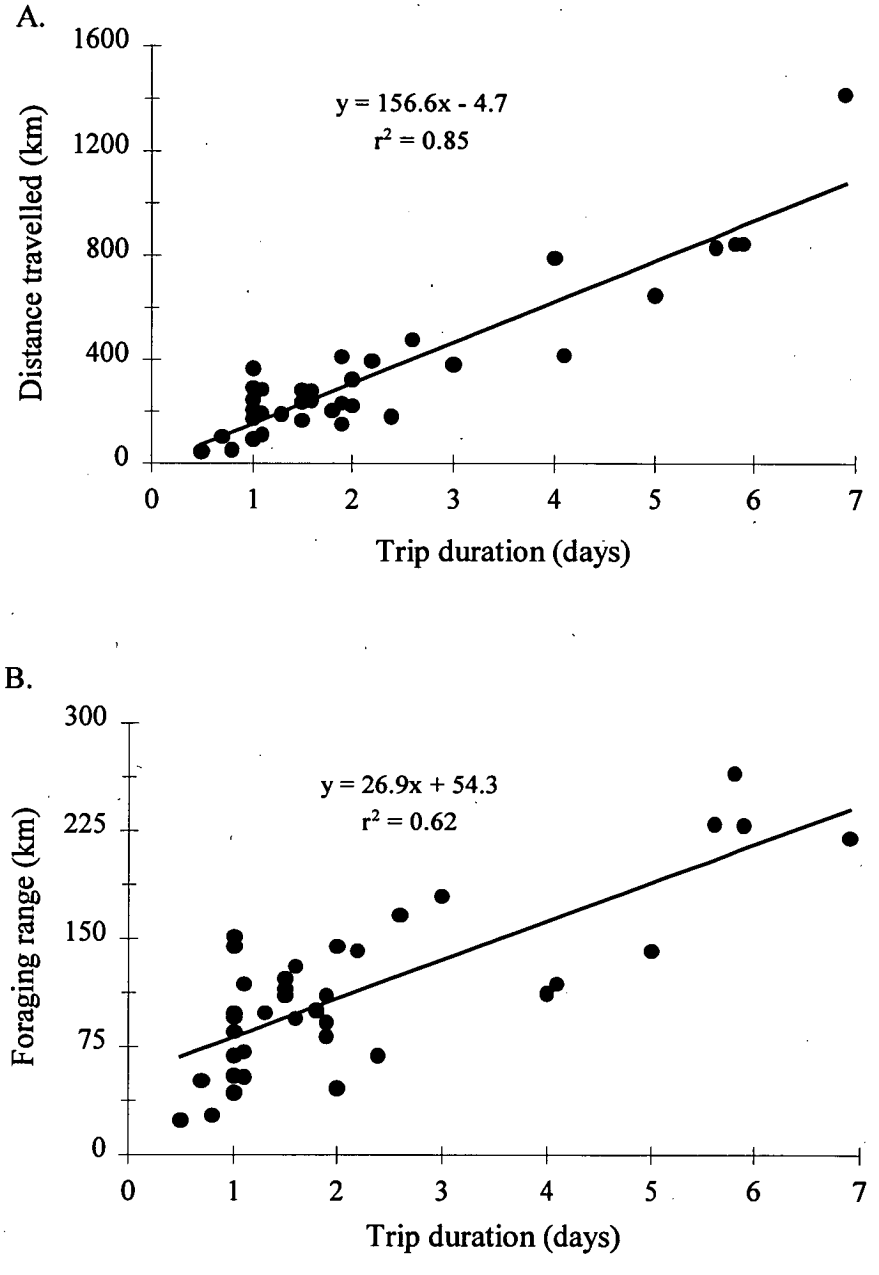

Figure 3.3: Relationship between trip duration and (A) the distance travelled and (B) the foraging range of breeding Shy Albatrosses on Albatross Island and Pedra Branca.

Table 3.3: Distance and duration of tracking sessions, and foraging range of post-breeding Shy Albatrosses (mean ± S.D., range and sample size). All birds were foraging at sea when transmissions ceased.

Period and location	n	Distance covered (km)	Foraging range (km)	Tracking period (days)
Post-breeding				
April-May 1994	4	2,515 ± 901	308 ± 125	23.7 ± 8.2
(Albatross Island)		1,463 - 3,525	195 - 475	12.4 - 32.1
Post-breeding				
March-April 1995	3	2,492 ± 852	501 ± 163	24.2 ± 1.2
(Pedra Branca)		1,568 - 3,247	350 - 673	22.9 - 25.1

Albatross Island during both early incubation and brooding in 1993, and from Pedra Branca during late incubation in 1994. When incubating, birds from Albatross Island used a foraging zone encompassing 27,700 km^2 of ocean over the Australian continental shelf (Table 3.4), with a high concentration of points (the centre of activity) 74 km west of the island (Figure 3.4). When rearing small chicks, the foraging zone used by Albatross Island birds was reduced to 18,900 km^2. In this instance the centre of activity was located just 9 km west of the colony. Although during the brooding phase the activity centre was considerably closer to Albatross Island than during incubation, analyses indicated that these foraging zones overlapped by 41% during 1993 (Figure 3.4) The foraging zone of late incubating birds from Pedra Branca was relatively small (9,500 km^2). Birds departed from the colony and headed east or southeast towards the edge of the continental shelf (Figure 3.4).

3.3.4.2 Post-breeding birds:

Post-breeding birds ranged more widely than breeders, and their foraging zones tended to be larger (Figure 3.5). Also notable was the wider separation of the centres of activity from the breeding sites (Table 3.4, Figure 3.5). Because post-breeding birds dispersed further, their foraging zones overlapped less than during the breeding season. Mean overlap between individual Pedra Branca birds was 19%, whilst it was 10% between birds from Albatross Island. An area off the northwest coast of Tasmania, which was used by one of the post-breeding birds from each colony, indicates the potential for overlap outside the breeding season. As can be seen in Figure 3.5B, 20% of the calculated

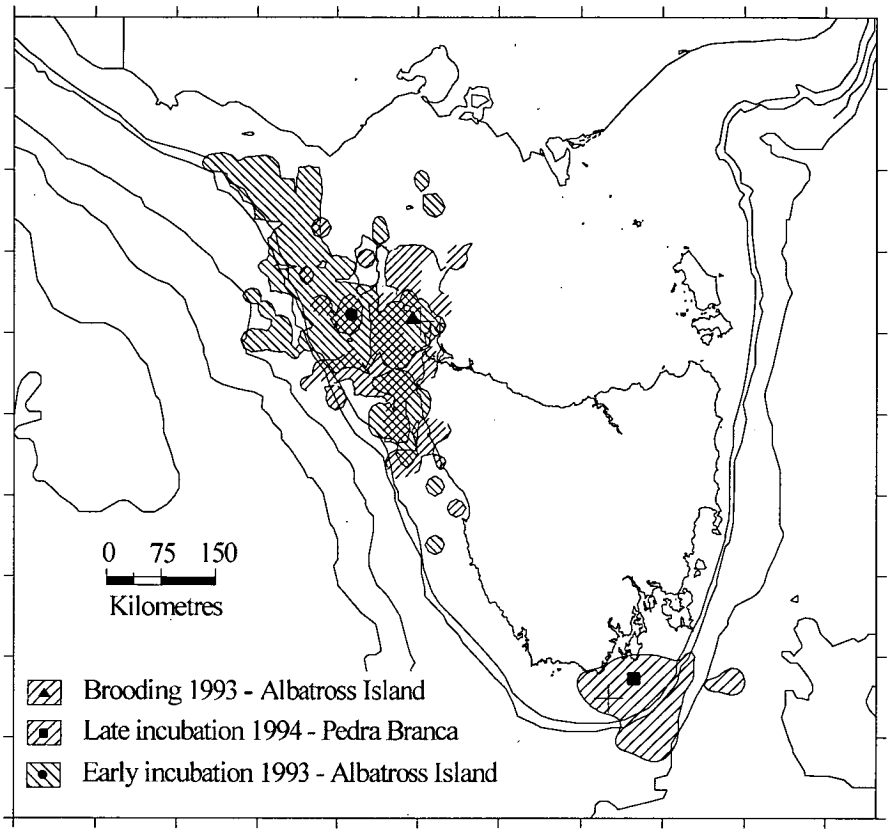

Figure 3.4. Foraging zones of breeding Shy Albatrosses assessed from Home Range Analyses. Each hatch pattern identifies the foraging zone of birds during different stages of the breeding cycle, and symbols denote the centres of activity.

foraging zone of individual 3 from Pedra Branca was over mainland Tasmania. As albatrosses obviously do not forage over land, the adjusted foraging zone of this bird was 35,809 km^2. The extent of error in this calculation can likely be accounted for by the individuals movement patterns, which were characterized by widely spaced locations with relatively few points of concentration. It seems likely that this spatial scattering could account for an overestimation of the area actually used.

Table 3.4: Foraging zones of Shy Albatrosses estimated from 95% isopleths of fixed Kernel home-range analyses during breeding (individuals pooled) and post-breeding (individual data) periods. Numbers associated with data for post-breeding birds refer to different individuals.

Tracking period & source breeding colony	Number of locations used	Foraging zone (km^2)	Centre of activity (km from breeding colony)
Early incubation 1993 (Albatross Island)	209	27,700	74
Chick brooding 1993 (Albatross Island)	113	18,900	9
Late incubation 1994 (Pedra Branca)	82	9,500	27
Post-breeding (1) 1994 (Albatross Island)	99	32,800	381
Post-breeding (2) 1994 (Albatross Island)	118	8,800	61
Post-breeding (3) 1994 (Albatross Island)	149	5,300	195
Post-breeding (4) 1994 (Albatross Island)	100	8,400	102
Post-breeding (1) 1995 (Pedra Branca)	134	47,500	618
Post-breeding (2) 1995 (Pedra Branca)	215	8,700	282
Post-breeding (3) 1995 (Pedra Branca)	206	44,700	37

3.3.5 Relationship of Flight Patterns to Wind

Birds did not fly more with tail or side winds than against head winds (χ^2_2=4.75, $p > 0.05$). However, when birds covered relatively large distances (> 20 km) or when winds were particularly strong (> 30 km/h) the associations were significant (χ^2_2=5.9, $p < 0.05$, and χ^2_2=7.1, $p < 0.05$). There were no differences in the travelling rates or the distances

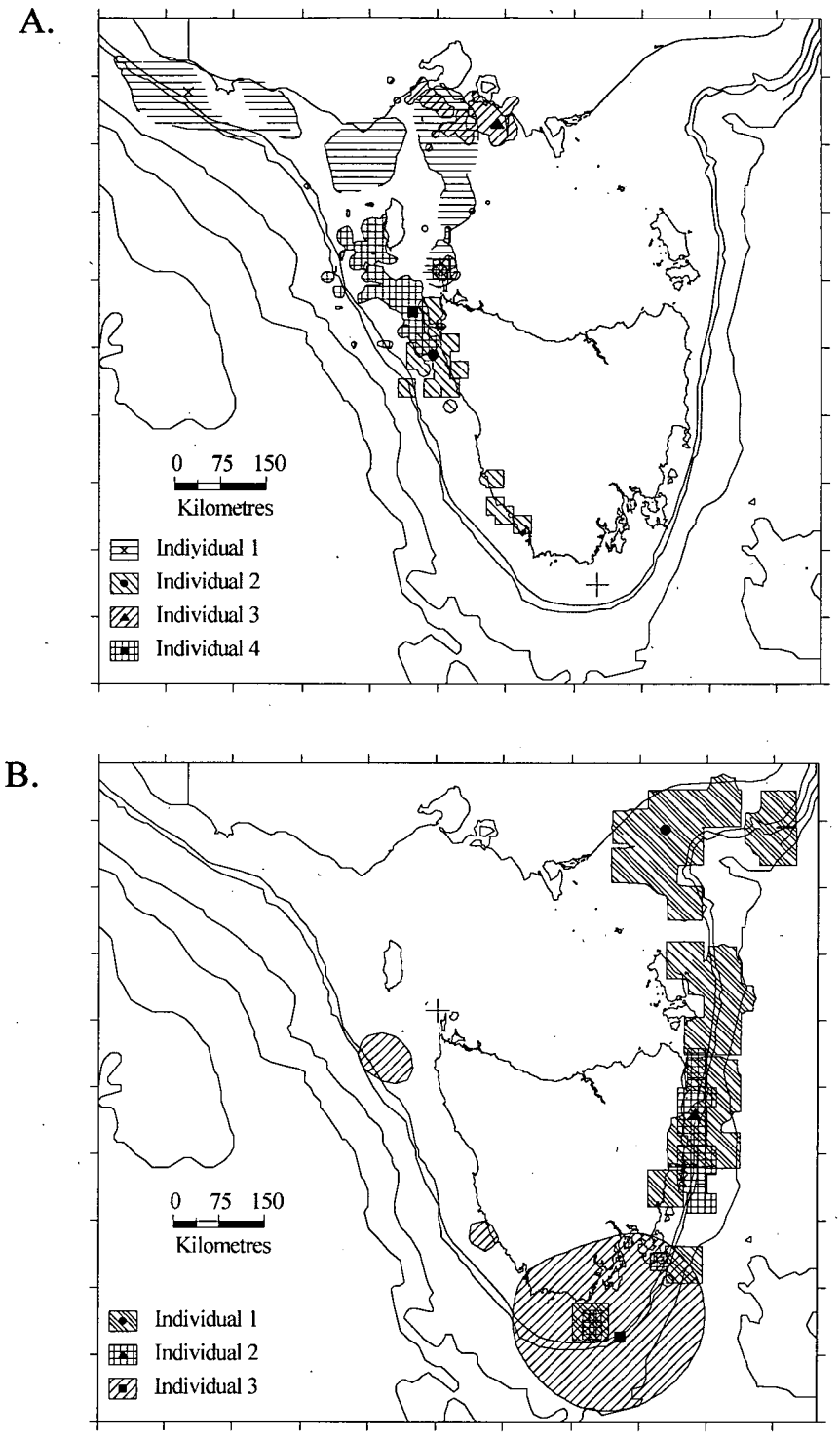

Figure 3.5: Foraging zones of post-breeding Shy Albatrosses from (A) Albatross Island in April-May 1994 and (B) Pedra Branca in March-April 1995, as assessed using Home Range Analyses. Each hatch pattern identifies the foraging zone of a different individual, and symbols denote the centres of activity.

covered by birds flying with tail or side (favourable) as opposed to head winds (one-way ANOVA, $F_{2,532}=1.5$, $p > 0.05$, and $F_{2,532}=0.5$, $p > 0.05$).

3.3.6 *Albatross-Fishery Interactions*

Depiction of simultaneous overlap of Shy Albatrosses with the Japanese Southern Blue-fin Tuna fishery is provided in Figure 3.6 A-E. Breeding birds from Pedra Branca overlapped extensively with the Japanese Southern Blue-fin Tuna fishery off the southeast coast of Tasmania, where hooks were set in all of the 1° grid squares used by the birds. During the actual tracking periods, however, there was no overlap between this fishery and birds breeding on Albatross Island nor with postbreeding birds from either colony. The brevity of the tracking periods (covering just 14% and 7%, and 18% and 15 % of the 1993/94 and 1994/95 breeding and non-breeding seasons, respectively), however, makes examining just the simultaneous overlap misleading. When the Japanese fishing effort is considered through the full breeding (September- April) and non-breeding period (April-August; total effort, Figure 3.7), the extent of fishing potentially occurring in the foraging zones of the Shy Albatross is, in fact, considerable. In the nonbreeding season, hooks were set off Tasmania's west coast in 13% (2 of 16) of the grid squares used by post-breeding birds from Albatross Island, and off the south, north and east coasts in 43% (9 of 21) of the areas used by post-breeding birds from Pedra Branca. During the full breeding period, birds from Albatross Island could again potentially overlap with this fishery off the west coast of Tasmania, where hooks were set in 6% (1 of 18) of the areas used. As with the simultaneous overlap, fishing occurred off the southeast coast of Tasmania in all areas used by birds breeding on Pedra Branca.

3.4 DISCUSSION

3.4.1 *Foraging Zones of Shy Albatrosses*

Breeding adult Shy Albatrosses are relatively sedentary, travelling and feeding over the continental shelf, within 300 km of their breeding colonies. During the majority of foraging trips, birds from Albatross Island foraged in water less than 200 m deep and only occasionally traversed continental slopes. Breeding birds from Pedra Branca, however, tended to travel east or southeast towards the edge of the shelf.

3.4.2 *Foraging Behaviour in Relation to Breeding Stage*

Differing to other species of albatross studied, Shy Albatrosses in Australia can be

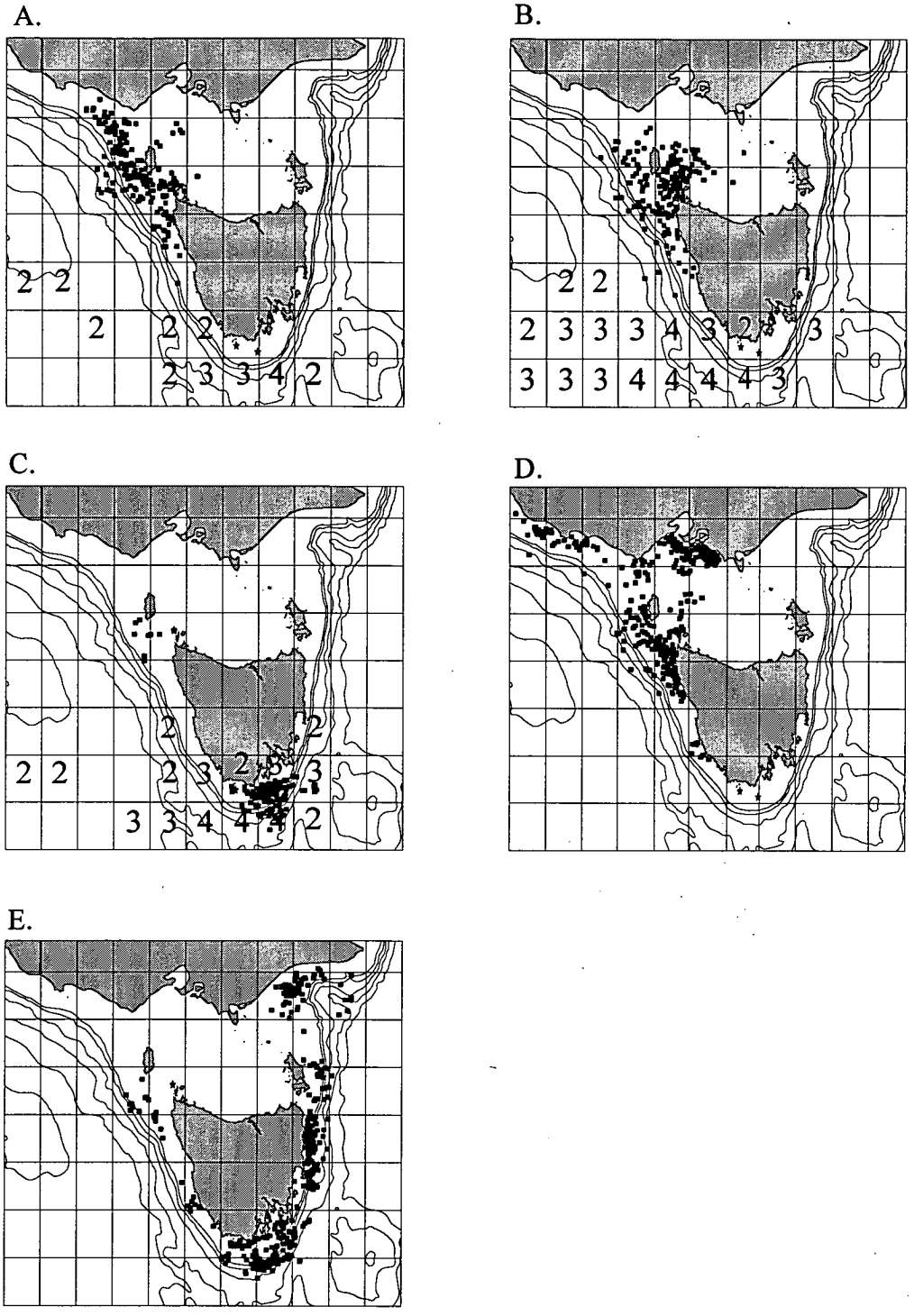

Figure 3.6: Foraging tracks of Shy Albatrosses relative to Japanese fishing effort in the AFZ during (A) early incubation (September) from Albatross Island in 1993; (B) brooding (December) from Albatross Island in 1993; (C) late incubation and brooding (December) from Pedra Branca in 1994; (D) the post-breeding period (April-May) from Albatross Island in 1994; and (E) the post-breeding period (March-April) from Pedra Branca in 1995. Numbers in each 1° x 1° grid square represent the number of hooks set during the tracking period, as follows: 1=1-999, 2=1,000-9,999, 3=10,000-99,999, 4=100,000-999,999, 5=1-2 million, 6=over 2 million. A blank cell indicates that no hooks were set.

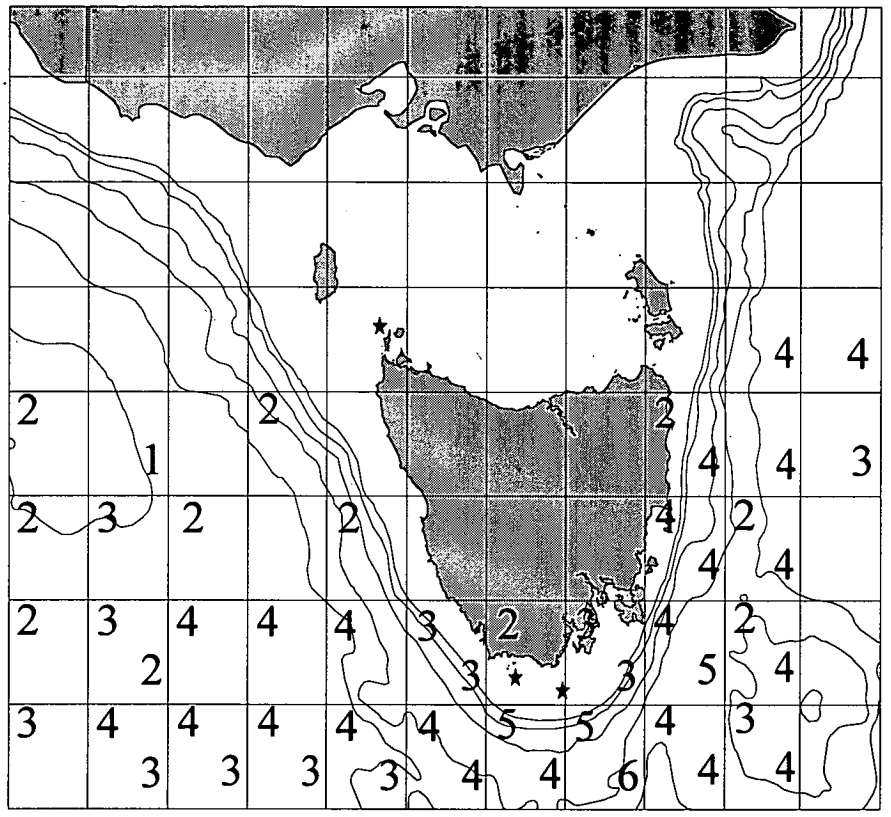

Figure 3.7: Total hooks set by the Japanese Southern Blue-fin Tuna fleet off Tasmania in 1993/94 and 1994/95 during Shy Albatross breeding (numbers in the top left hand corner of each grid square) and post-breeding periods (numbers in the bottom right hand corner of each grid square). Numbers correspond to the total number of hooks set during these periods and equate to those in Figure 3.6.

characterized as having relatively local movements both during and subsequent to the breeding season. The distances travelled by these birds and the duration of time spent at sea are less than reported for other species, but changes in the foraging pattern throughout the breeding cycle are broadly similar (Tickell & Pinder 1975, Weimerskirch et al. 1986, Weimerskirch et al. 1993). Foraging trip duration and the distances travelled were longest early in incubation, shortened progressively as hatching approached, and were further reduced through the brooding period when chicks were fed every day or two.

3.4.3 *Rate of Travel and the Influence of Winds*

The relatively short distances covered by Shy Albatrosses perhaps account for differences in travelling speeds relative to species which forage further afield. Using comparable data of known accuracy, the maximum travelling speed recorded for this species was 27.8 km/h, much less than the 80-90 km/h rates recorded for both Wandering Albatrosses (Prince et al. 1992, Weimerskirch et al. 1993, Walker et al. 1995) and Light-mantled Sooty Albatrosses *Phoebetria palpebrata* (Weimerskirch & Robertson 1994), and less than the theoretical maximum speed (68 km/h) calculated from Pennycuick's equations (Program 1, 1989). It may be argued that lower apparent flight speeds could be attributed to the infrequent locations (5.6 per day) were it not for the fact that, even when tracking signals were separated by less than 1 hour, calculated travelling speeds never exceeded 30 km/h. Proximity of the foraging grounds to the breeding colony and limited opportunity to exploit winds as strong as those encountered by birds foraging 50-60° S perhaps account for the less extensive and less rapid travelling behaviour of Shy Albatrosses. Shy Albatrosses tend to use winds only when they move over large distances or when the winds are strong. Wind is important to species such as Wandering Albatrosses which search vast expanses of open ocean in search of patchily distributed prey during extended inter-incubation and chick-rearing trips (Weimerskirch et al. 1993). Wind is also important in determining the routes of highly migratory albatrosses outside the breeding season (Nicholls et al. in press).

3.4.4 *Foraging Zones*

The oceanic areas used by albatrosses fall into two categories; (1) areas identifiable from their oceanographic or bathymetric features, such as continental shelves or slope breaks and (2) pelagic waters with no such features (Weimerskirch et al. 1993, Weimerskirch & Robertson 1994, Cherel & Weimerskirch 1995, Walker et al. 1995, Sagar & Weimerskirch 1996, Prince et al. in press, Weimerskirch in press). The foraging

strategies and areas prospected vary greatly between species, as well as within species through breeding and post-breeding cycles (Weimerskirch et al. 1993, Weimerskirch et al. 1994, Weimerskirch in press).

Satellite tracking of five albatross species (Wandering, Light-mantled Sooty, Sooty *Phoebetria fusca*, Buller's *Diomedea bulleri*, and Black-browed *Diomedea melanophris*) reveals basic foraging strategies that can be clustered into two major groups (Weimerskirch in press). The first centres on "commuting", birds moving rapidly to specific oceanic sectors where most of the time is spent before return to the breeding colonies. These trips can be short or long. The second centres on "searching", with the birds moving continuously throughout their foraging trips. Based upon the data presented here, Shy Albatrosses appear to use the searching strategy, following both looping and linear courses over the Australian continental shelf and slope waters off Tasmania. However, as the brevity of foraging trips, in terms of both distance and time, could mask "commuting" behaviour, this characterisation must be considered preliminary.

In terms of both the distances travelled and the areas prospected, Shy Albatrosses are similar to Black-browed Albatrosses, which also undertake 2-3 day foraging trips over shallow waters throughout the breeding season (Cherel & Weimerskirch 1995, Prince et al. in press, Weimerskirch in press). However, in contrast to the searching strategy employed by Shy Albatrosses, Black-browed Albatrosses from Kerguelen Island (Cherel & Weimerskirch 1995, Weimerskirch in press) and South Georgia (Prince et al. in press) commute both rapidly and directly to continental shelf breaks or frontal zones. Black-browed Albatrosses from Kerguelen Island revisit the same areas on successive trips, indicating the highly predictable nature of their prey (Cherel & Weimerskirch 1995, Weimerskirch in press). During the breeding season, Shy Albatrosses forage within 300 km of their breeding colony. While they range further outside the breeding season, they remain over the continental shelf off southeast Australia. Prey must therefore be both sufficiently predictable and abundant in this region to support their annual energy requirements.

Many of the foraging zones reported here for Shy Albatrosses lie within Bass Strait. This is a sector of continental shelf between the coasts of Victoria and Tasmania at depths of 50 to 100 m (Figure 3.2). The distribution of nutrients in the area is closely related to physical processes occurring over the continental slopes at the eastern and western edges of the Strait. Throughout the year, the highest relative concentrations of phytoplankton biomass are found at the southwest extremity between King Island and Cape Grim (west of Albatross Island) and at the eastern shelf break near Flinders Island, with overall levels

peaking during winter (Gibbs et al.1986, Gibbs 1992). Discontinuities in water temperature also indicate sporadic upwelling of nutrient rich sub-Antarctic waters into areas surrounding Albatross Island, which are used extensively by birds during the breeding season (Blackman et al. 1987). Waters to the south and east of Tasmania, used by birds from Pedra Branca, are also nutrient rich (Young et al. 1995). This high productivity results from a mixing of the inner edge of the south-flowing eastern Australia current with the Zeehan current and nutrient-rich subantarctic waters (Young et al. 1995). Peaks in phytoplankton biomass occur in Spring (October) and Autumn (April), with lower levels observed during the winter months (Harris et al. 1987). These high levels of productivity, and their predictability, likely contribute to the sedentary habits of adult Shy Albatrosses in the region.

3.4.5 *Interactions with Fisheries*

This study, together with observations at sea (Reid et al. in press) and sightings of colour-marked birds and ringing recoveries (Brothers et al. in press), indicates that adult Shy Albatrosses which breed in Australia remain in the waters off southeast Australia all year round. The increased concentration of Japanese longlining effort off the south and east coasts of Tasmania and the concomitant increase in the Australian domestic longline fishery in the region is consequently of considerable concern. The provenance of just five of the 400-1,500 Shy Albatrosses estimated to be killed annually in the Japanese longline fishery within the AFZ is known. Three of these birds originated from the Mewstone, south of Tasmania, and two were ringed on Albatross Island in the north (Gales et al. unpubl. data). Although it seems likely that some of the birds killed must be from New Zealand (Brothers et al. in press), the difficulty of distinguishing Australian and New Zealand Shy Albatrosses makes it impossible to adequately assess the impact of this mortality on either species. As Japanese longline fishing is concentrated mainly off the south and east coasts of Tasmania, there is less potential for overlap than with adult birds from Albatross Island. Birds breeding south of Tasmania (Pedra Branca and the Mewstone), forage all year long in areas used by Japanese longliners, leaving them vulnerable throughout the year. These differential threats clearly demonstrate the importance of examining fisheries interactions at the population level. Shy Albatrosses are also killed in the Australian domestic longline fishery off Tasmania (Brothers & Foster in press), but, as the distribution of effort in this fishery and the magnitude of the bycatch is unknown, the relative vulnerability of birds at the different sites cannot be assessed.

Whilst longline fishing has been identified as the most serious threat facing albatrosses, other fishing practices are also known to have an impact. Most notably for the locally breeding Shy Albatrosses are the South East Trawl, the Southern Rock Lobster *Jasus edwardsii* and the Dropline Fisheries. Shy Albatrosses are known to follow fishing boats, scavenging both baits and offal discharge, and their at-sea distribution is influenced by such activity (Bartle 1974, Ryan & Moloney 1988). Albatrosses and other marine vertebrates are also shot to reduce scavenging from both trawl and dropline fisheries within Australian waters. As the extent of such activities are unknown, their likely effects cannot be quantified.

3.4.6 *Population Status*

While at Albatross Island Shy Albatross numbers are increasing, there is no data available for population trends at the other breeding sites (Gales in press). At Albatross Island, numbers are increasing following heavy human exploitation during the 19th and early 20th centuries when birds were killed for their feathers. In 1994/95, approximately 5,000 pairs bred on the island (Gales in press). Although favourable, this is substantially less than the 20,000 pairs estimated by Brothers to have bred there early in the 19th century (N Brothers, unpubl. data). Any longline-induced mortality could reasonably be expected to curtail this recovery. The status Shy Albatrosses breeding on the Mewstone and Pedra Branca is unknown, but due to extensive overlap with longline fisheries, is of concern.

Juvenile and immature Shy Albatrosses from Australia cover greater distances than adults and their at-sea distribution appears specific to the natal colony (Brother et al. in press). Birds from Albatross Island have been found only as far west as southwest Western Australia, while young birds from the Mewstone have been recovered off both South Africa and New Zealand. As the dispersal of young birds potentially exposes them to a greater number of fisheries than those which threaten the adults, further research into their at-sea distribution is of high priority.

3.5 ACKNOWLEDGMENTS

We are grateful to Catherine Bone, John Grant, David Pemberton, and Jenny Scott for help in the field, to Neil Smith for transport to and from the islands, and to Lee Hedd for his help in preparing the figures. Christophe Guinet, Mark Hindell, Cindy Hull and David Ritz improved earlier drafts of the manuscript. Financial support was provided by the Tasmanian Parks and Wildlife Service, the Australian Nature Conservation Agency, the

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Chapter 4

DIVING BEHAVIOUR OF THE SHY ALBATROSS *Diomedea cauta* IN TASMANIA: INITIAL FINDINGS AND DIVE RECORDER ASSESSMENT

April Hedd, Rosemary Gales, Nigel Brothers & Graham Robertson

4.1 INTRODUCTION

The diving behaviour of seabirds has been extensively investigated during the last decade primarily due to the increasing use of maximum depth gauges (MDGs), and more recently the miniaturization of time-depth recorders (TDRs). Coupled with dietary information, knowledge of diving patterns and performance can provide insight into seabird foraging ecology. Diving capability limits the prey available to seabirds, and must be quantified in order to correctly interpret foraging dynamics. MDGs or capillary tubes (Burger & Wilson 1988) provide an inexpensive means of providing this information, and both their low cost and small size has resulted in widespread application. Groups studied using this technique include penguins (Whitehead 1989, Seddon & van Heezik 1990), alcids (Burger & Powell 1990, Burger 1991), gannets (Adams & Walter 1993), petrels (Prince & Jones 1992), and albatrosses (Prince et al. 1994).

Albatrosses are not generally regarded as divers due to their propensity for economic, long-distance flight (Pennycuick 1987) and their large body size. Indeed, most observations of albatrosses feeding at sea are of birds on the surface seizing dead or moribund prey (Harper et al. 1985, Croxall & Prince 1994), or occasionally, making shallow dives or surface plunges in search of fisheries discards (Prince 1980, Prince & Morgan 1987, Thompson 1992). The recent study using MDGs (Prince et al. 1994), and other direct observations of albatrosses at sea (Nicholls 1979, Harper 1987, N Brothers, unpubl. data), however, suggest that diving may form a typical part of albatross foraging behaviour. Four of the five albatross species studied by Prince et al. (1994) exhibited mean maximum diving depths of 2.5 m or greater. The smaller Light-mantled Sooty Albatrosses *Phoebetria palpebrata* dived to a mean maximum depth of 4.7 ± 3.4 m, and individuals reached up to 12.4 m.

This paper details the diving behaviour of the Shy Albatross *Diomedea cauta* gathered using both MDGs and TDRs. To properly interpret these data, the TDRs and MDGs were subjected to a variety of diving simulations designed to test both their accuracy and

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suitability for studies of albatross diving behaviour. Data were also gathered in the field from both simultaneous and independent deployments of the TDRs and MDGs, and interpretation of errors associated with these methods are discussed. While the data reported here are of interest in studies of feeding ecology, the diving capability of albatrosses must also be considered when assessing their susceptibility to incidental capture in longline fisheries as well as for the design of appropriate mitigation measures (Brothers 1991).

4.2 METHODS

4.2.1 *Study Sites and Species*

Fieldwork was carried out in Tasmania, Australia, on Albatross Island (40 ° 24' S; 144° 32 ' E) in western Bass Strait during the brooding periods in December 1993 and 1994, and from Pedra Branca (43 ° 52' S; 146 ° 58 ' E) south of Tasmania, during late incubation and early chick brooding in December 1994. Shy Albatrosses breed annually on these islands, and egg-laying commences in September (N Brothers, unpubl. data). However, breeding is not synchronized at the two sites, with the mean egg-laying date at Pedra Branca being approximately 1-2 weeks later than on Albatross Island (N Brothers, unpubl. data). Eggs are incubated for approximately 10 weeks, and chicks hatch in December. Chicks are brooded by both parents for approximately three weeks, and fledge during April. Shy Albatrosses are sexually dimorphic, with adult males being slightly larger and heavier than females (N Brothers, unpubl. data). The only published information regarding the diet of this species comes from 75 regurgitates collected from chicks approaching fledging on Albatross Island during April 1973 (Green 1973). Fish occurred most frequently, being present in 59% of the samples, followed by cephalopods (53% of samples), crustaceans (35% of samples) and tunicates (32% of samples).

4.2.2 *Experimental Protocol*

4.2.2.1 *Maximum Depth Gauges*

Diving simulations were conducted to assess the effects of dive depth, duration, frequency and descent rate upon MDG accuracy. Although Burger & Wilson (1988) previously reported errors associated with MDGs, it was necessary to more intensively examine their accuracy at shallow depths. Tests were conducted in a 3.16 m tank filled with 14 °C seawater.

Tests for depth accuracy were performed by lowering three MDGs, for 10 seconds each, to nine depths between 0.20 and 3.16 m. To assess the effect of dive duration, three gauges were lowered to shallow (0.16 m), moderate (1.65 m) and deeper depths (3.16 m) for intervals ranging from one second to one hour. Errors resulting from variations in diving frequency were investigated by lowering three gauges to the depths indicated above either 1, 5, 10 or 50 times. Gauges were again held at depth for 10 seconds.

The effect of descent rate was examined by submerging three gauges at speeds ranging from 0.3 to 1.1 m/s to the three depth categories indicated above. Descent rate was calculated by noting both the time the instrument first contacted the water and the time it reached the tank bottom.

Depth gauges were made from flexible Tygon ® tubing, approximately 100 mm long, with an internal diameter of either 1.0 or 1.6 mm. Tubes were coated internally with a thin layer of seived icing sugar and sealed at one end with quick setting epoxy (Bostik, Epoxy Bond, 5 Minute). The length of tubing covered with sugar was measured both initially and after tubes were recovered, and the maximum depth was calculated from the following formula (Burger & Wilson 1988); $d = 10.08(L_s/L_d - 1)$, where d is depth in m, L_s is the original length of tube-wall coating, and L_d the length of coating remaining following deployment. For all simulations, depths calculated from the MDGs were compared to the known submergence depths.

4.2.2.2 *Time Depth Recorders*

Five Mk5 TDRs (Wildlife Computers, Washington, USA) with a depth resolution of 0.10 m (to a maximum depth of 25 m), were designed specifically to record albatross diving behaviour. The TDRs measured 62 mm (long) x 35 mm (wide) x 13 mm (high) and weighed 39 g (equivalent to 0.8 -1.1 % of the adult body mass).

Experiments were conducted to assess the accuracy of the TDRs depth and time components. Tests for TDR depth accuracy were similar to those outlined above for MDGs, but were repeated in triplicate at each of nine depths between 0.20 and 3.16 m. Recorders were maintained at the target depths for 5, 10 or 20 seconds. The TDRs internal clock was tested by submerging TDRs in seawater for intervals ranging from 5 seconds to 30 minutes. The recorded dive durations were compared to stopwatch measurements.

4.2.3 *Field Protocol*

4.2.3.1 *Maximum Depth Gauges*

Maximum depth gauges were deployed between 5-14 December 1993 from Albatross Island, and in conjunction with TDRs from Pedra Branca between 4-16 December 1994.

Experiments conducted during 1993 assessed the precision of the MDGs as well as the effect of body placement. MDGs were deployed either singly, attached to the birds back or metal leg band, or in sets of two or three where gauges were placed on one or both of the legs and/or upon the bird's back. Gauges were either coiled and taped around the leg bands, or taped directly to feathers on the back.

In 1994 MDGs were taped to TDRs and both were attached to the bird's back. Data comparing the calculated (MDG) and known maximum depths (TDR) are available for seven albatrosses.

4.2.3.2 *Time Depth Recorders*

TDRs were deployed on 15 occasions and data collected during 20 foraging trips between 02-16 December 1994. Birds were caught and TDRs attached as they returned to sea, following being relieved of incubation or brooding duties by their partners. Birds were ringed and colour marked for identification upon return to the colony. Colony attendance checks were made at a maximum of two hours, and observations were often continuous during daylight to obtain precise departure and arrival times.

TDRs were attached directly to feathers on the dorsal midline using TESA ® tape, and were programmed to record depth every second, light and temperature every 15 minutes, and the total time spent either wet or dry. Light level and ambient temperature were recorded every 15 minutes when the bird was at the surface, and the TDRs conductivity sensor (salt-water switch) determined whether the device was submerged.

All dive data were analyzed using Wildlife Computers Software (Redmond, WA, USA). While the TDRs had a depth resolution of 0.10 m, it was not clear that depth changes of 0.30 m or less could be distinguished from noise at the surface. The depth of surface readings also drifted during deployment, making it necessary to manually adjust the position of the zero line. For these reasons, the analysis of diving behaviour was restricted to instances where depth changes were $\geq$ 0.40 m. However, when calculating the

proportion of the day and night the birds spent in or on the water, no such restrictions were imposed.

Statistical analyses were performed using either NCSS (Kaysville, Utah, USA) software version 5.03, or SYSTAT for Windows, version 5.03 (Evanston, IL, USA). Data are reported as means ± 1 S.D. as appropriate.

4.3 RESULTS

4.3.1 *Experimental Data*

4.3.1.1 *Maximum Depth Gauges*

When lowered into the water for 10 seconds, depths calculated by MDGs were similar to the known submergence depths (paired t-test t_{36}= -0.3, p>0.05). However, at depths less than 0.50 m a number of gauges failed to record diving activity, and errors up to 100% were evident (Figure 4.1A). The accuracy of estimates increased with increasing depth, and the error rate was always less than 25% for depths greater than 0.50 m. The effects of varying the diving parameters, and their interaction with depth, were investigated. All data were expressed as a percentage deviance from actual depth. Increasing the dive duration decreased the accuracy of depth predictions (Figure 4.1B; two-way ANOVA $F_{4,30}$=8.8, $p < 0.001$), with data from the one hour trials being proportionately worse than those from the shorter trials (Fisher's LSD, $p < 0.05$). The mean error also varied with depth category (two-way ANOVA $F_{2,30}$=56.1, $p < 0.0001$), being higher for the most shallow depths (Fisher's LSD, $p < 0.05$). A significant interaction existed between dive duration and depth (two-way ANOVA $F_{8,30}$=6.2, $p < 0.001$), with the poorest overall predictions (mean error = 167%) resulting from the longest, most shallow dives (1 h at 0.16 m).

The proportion of error also increased with an increase in diving frequency (Figure 4.1C; two-way ANOVA $F_{3,22}$=4.5, $p < 0.05$), being significantly greater after 50 dives (Fisher's LSD, $p < 0.05$). Error rates again varied with depth category, being proportionately higher for the shallowest dives (two-way ANOVA $F_{2,22}$=37.6, $p < 0.0001$). A significant interaction existed between diving frequency and depth (two-way ANOVA $F_{6,22}$=2.9, $p < 0.05$), with the poorest predictions (mean error = 226%) resulting from the highest diving frequency at the shallowest depth. Varying descent rate had no effect (Figure 4.1D; two-way ANOVA $F_{2,18}$=1.2, p>0.05), however, predictions were generally poor for the

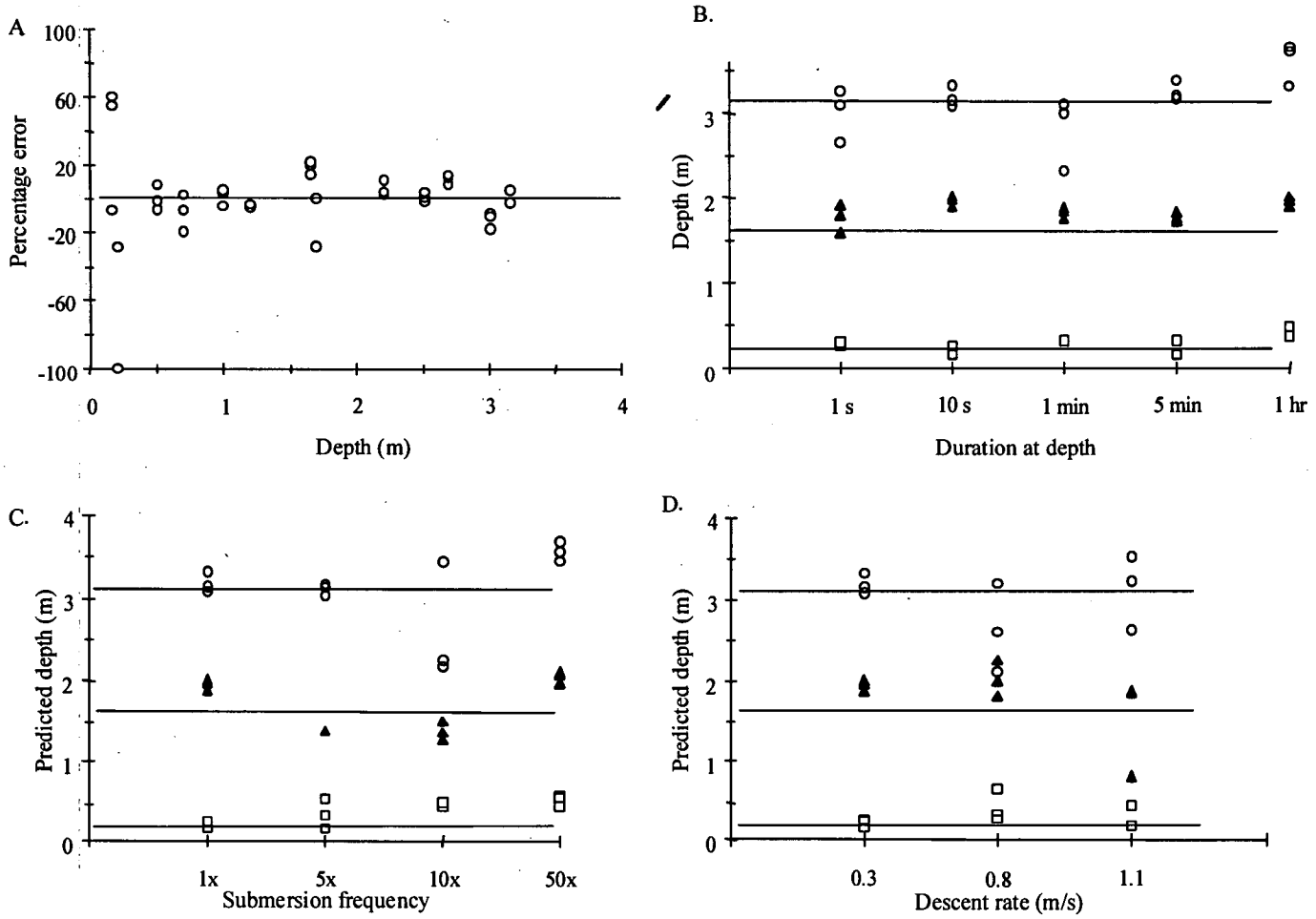

Figure 4.1: Data gathered from MDGs during the diving simulations. (A) Percentage of error when gauges were submerged once to the indicated depths. Predicted depths (m) when gauges were lowered to shallow (□), moderate (▲) and deep (O) depths (B) for intervals ranging from 1 second to 1 hour, (C) either 1, 5, 10 or 50 imes, and (D) at speeds ranging from 0.3 to 1.1 $m.s^{-1}$.

shallowest depths (two-way ANOVA $F_{2,18}=6.4$, $p < 0.01$).

4.3.1.2 *Time Depth Recorders*

Small-scale fluctuations (± 0.10 m) were evident during the TDR calibrations, but these were always within the stated resolution of the device (± 0.10 m). Pooling data for all TDRs over the depth trials revealed a significant difference between TDR and actual depth (paired t-test $t_{314}=38.4$, $p < 0.0001$), but again, this variation was within the devices resolution (± 0.10 m) for each interval tested. The TDRs time component was highly accurate, averaging 0.5 seconds less than the stop-watch calculated intervals over 95 time trials.

4.3.2 *Field Data*

4.3.2.1 *Maximum Depth Gauges*

Of 80 gauges deployed, 67 (84%) were recovered with useable information. This data set contained 31 albatrosses for which maximum depth was determined from a single gauge and 17 instances where maximum depths were determined from multiple gauges. The mean maximum dive depth of Shy Albatrosses recorded from all MDGs was 6.6 ± 10.0 m (n=67). Mean maximum dive depth calculated from the leg-placed MDGs (8.9 ± 11.4 m, n=47), was much greater than that calculated from gauges placed on the bird's backs (1.6 ± 1.1 m, n=21; one-way ANOVA $F_{1,65}=8.6$, $p < 0.01$).

When two MDGs were deployed simultaneously, the degree of correspondence depended upon the placement on the body. When two gauges were placed, one on each leg, values were highly comparable (paired t-test $t_5 = -1.0$, $p>0.05$). But, when one gauge was placed on the birds leg and another on its back, values for the former were 5.4 times greater (8.0 ± 8.0 m, n=6 *v* 1.5 ± 1.0 m, n=6; paired t-test $t_{12} = 3.2$, $p < 0.01$).

4.3.2.2 *Time Depth Recorders*

Details of the breeding colony, and descriptive statistics for the dives recorded from each albatross are given in Table 4.1. Although just 9 of the 15 birds dived deeper than 0.4 m, the TDRs conductivity sensor indicated that birds contacted the water on all foraging trips. Figure 4.2 provides an example of the data collected.

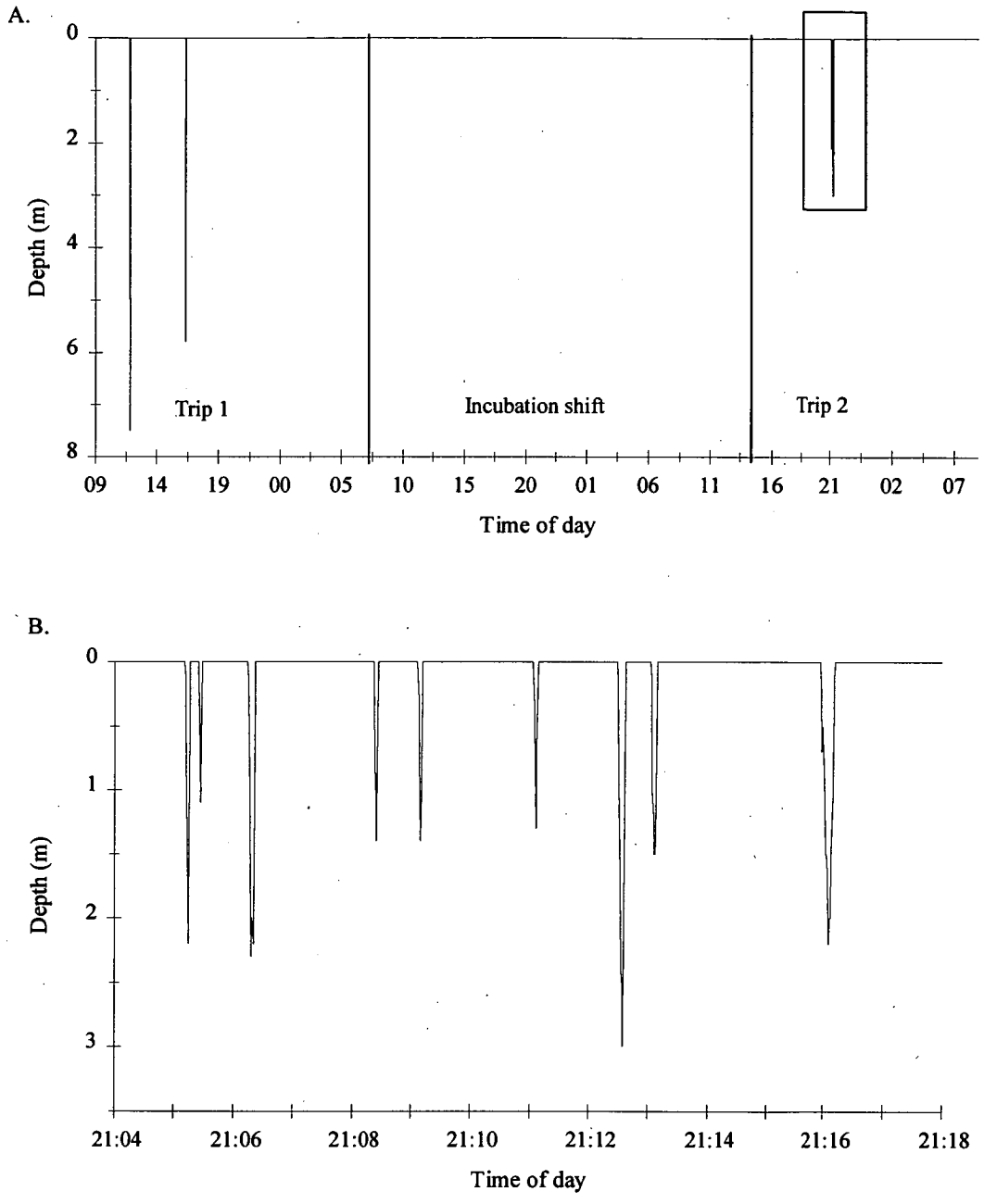

Figure 4.2: Diving record of a Shy Albatross collected during the incubation period in December 1994. (A) The entire three day record for this bird and (B) an enlargement of the boxed area indicated in section A.

Fifty-two dives (≥ 0.4 m) averaging 1.9 ± 1.7 m were recorded. Although the majority (87%) of dives were less than 3.5 m (Figure 4.3A), a number of deeper dives were recorded.

Maximum dive depth was 7.4 m, with four additional dives exceeding 5.0 m. Dives occurred between 0700 and 2200 h (10 h ahead of GMT), with peaks in diving activity occurring near midday and during twilight (χ^2_{13}=69.4 $p < 0.001$; Figure 4.3B). Overall, 64% of dives during twilight occurred 3-4 days prior to a full moon. Dive duration was generally short, averaging 4.4 ± 4.7 seconds, however, dives as long as 19 seconds were recorded (Figure 4.3C). A one-way ANOVA indicated that mean dive depth varied throughout the day ($F_{7,44}$=7.1, $p < 0.0001$) with birds diving to the greatest depths between 1000 and 1200 h (Fisher's LSD $p < 0.05$; Figure 4.4).

Table 4.1: Details of the breeding colony (1=Albatross Island; 2=Pedra Branca) and status (I=Incubating; B=Brooding), length of TDR deployment, number of foraging trips, number of dives, and the range of dive depths and durations recorded from Shy Albatrosses during December 1994.

Breeding colony & (status)	Deployment duration (days; # trips)	Total dives (n)	Depth range (m)	Range of diving duration (s)
1 (B)	0.8 (1)	3	0.9 - 1.4	2 - 4
1 (B)	1.9 (1)	2	0.7 - 2.0	2 - 3
1 (B)	2.5 (1)	0	-	-
1 (B)	2.7 (1)	2	0.4 - 0.7	1
1 (B)	1.3 (1)	12	0.4 - 2.9	1 - 3
1 (B)	2.6 (1)	8	0.4 - 1.6	1 - 4
2 (I)	3.0 (2)	13	1.0 - 7.4	4 - 19
2 (I)	4.8 (2)	2	0.4 - 6.1	2 - 14
2 (B)	2.2 (1)	5	0.7 - 2.2	2 - 5
2 (B)	1.6 (1)	0	-	-
2 (B)	1.3 (1)	5	0.8 - 5.6	1 - 16
2 (B)	2.1 (1)	0	-	-
2 (I)	4.0 (3)	0	-	-
2 (B)	4.9 (2)	0	-	-
2 (B)	2.7 (1)	0	-	-
Mean ± s.d.	2.6 ± 1.2	3.5 ± 4.4		

A plot of dive depth against descent rate revealed two different dive types (Figure 4.5); those for which average descent rates always exceeded 1 m/s (n = 20; hereafter called "plunge" dives) and those which never exceeded 1 m/s (n = 32; called "swimming"

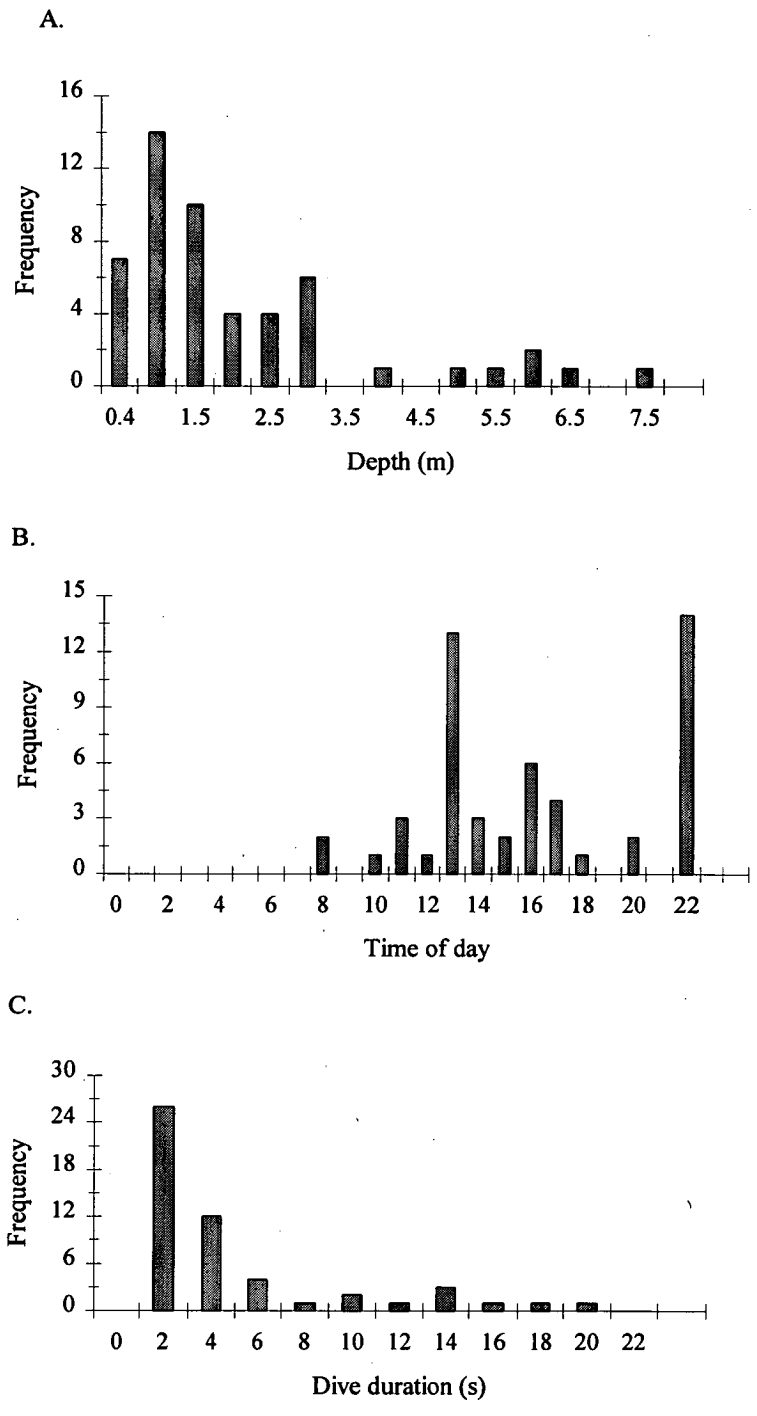

Figure 4.3: Histograms of (A) Dive depth, (B) Time of diving, and (C) Dive duration for Shy Albatrosses during late incubation and early chick-brooding in 1994.

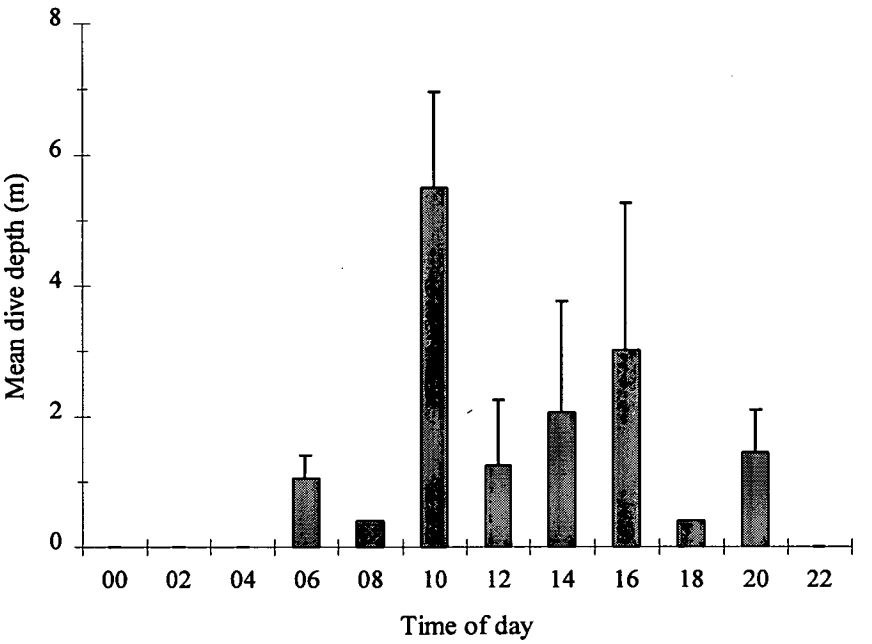

Figure 4.4: Mean dive depth (± S.D.) vs the time of day for Shy Albatrosses (n=9).

dives). The mean depth of plunge and swimming dives was similar (2.2 ± 2.0 m *v* 1.5 ± 0.8 m; one-way ANOVA $F_{1,50}$=2.3, p>0.05) although the latter lasted longer (6.0 ± 5.3 s *v* 1.9 ± 1.3 s; one-way ANOVA $F_{1,50}$=11.2, p < 0.01). The relationships between dive duration, depth and descent rate were different for swimming and plunge dives. Dive depth and descent rate were strongly correlated for plunge dives, but no relationship was evident between dive depth and duration (Figure 4.6 A,B); plunge dives tended to be short, five seconds or less, regardless of the depth reached. The reverse was true for the swimming dives; dive depth and descent rate were unrelated, but there was a strong relationship between dive depth and duration (Figure 4.6 C,D).

The proportion of time albatrosses spend in contact with water provides an index of feeding opportunity. Despite the fact that no dives occurred during complete darkness (2200-0500 h), the birds did spent a considerable amount of time in or on the water during these times. During daylight hours the birds spent an average of 6.7 ± 6.1% (n=15) of their time wet, not significantly different from the time spent in the water during the night (10.1 ± 11.8 % paired t-test t_{14}= -1.5, p>0.05) Birds spent an average of 7.9 ± 7.5 % (n=15) of their total time at sea with their back's submerged (Table 4.2).

Nested analyses of variance indicated that birds from Pedra Branca dived more deeply (2.7 ± 2.0 m (n=25) *v* 1.2 ± 0.8 m (n=27); $F_{1,43}$=9.4, p < 0.01) and for longer periods of time (7.3 ± 5.4 s *v* 1.7 ± 1.1 s; $F_{1,43}$=14.5, p < 0.001) than did birds from Albatross Island. Overall, this can be accounted for by the relative proportion of plunge and swimming dives from each location. Plunge and swimming dives were both common in the records of Albatross Island birds (59% vs 41%;χ^2_1 =0.9, p>0.05), whereas the former were relatively rare in Pedra Branca records (χ^2_1 =11.6, p < 0.001), accounting for just 16% of the total. However, differences in the diving characteristics within dive types were also apparent between the breeding sites. While there was no difference in the depth of plunge dives between Albatross Island and Pedra Branca birds (nested ANOVA $F_{1,6}$=0.9, p>0.05), those from Pedra Branca were longer (nested ANOVA $F_{1,6}$=6.1, p < 0.05). The swimming dives of Pedra Branca birds were both longer (nested ANOVA $F_{1,7}$=6.0, p < 0.05) and deeper (nested ANOVA $F_{1,7}$=6.4, p < 0.05) than those from birds breeding on Albatross Island.

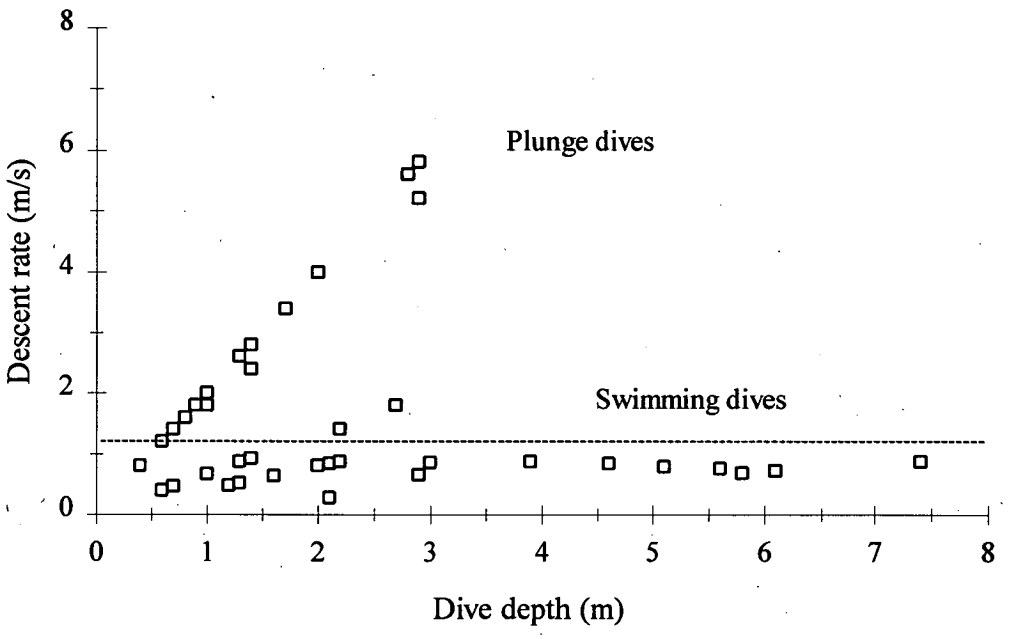

Figure 4.5: Relationship between dive depth and descent rate for all Shy Albatross dives (n=52). All dives lying below the dashed line are Swimming Dives, and those lying above it are Plunge Dives.

4.3.3 *Time Depth Recorder v Maximum Depth Gauge Data*

The mean maximum depths recorded from the TDRs (1.8 ± 2.2 m, n=20; assuming a maximum depth of 0.30 m for those albatrosses which did not dive deeper than 0.40 m) was significantly less than that recorded from the MDGs (one-way ANOVA $F_{1,85}=4.5$, $p < 0.05$). However, the mean maximum depth recorded from the TDRs is similar to that recorded from back-placed MDGs (one-way ANOVA $F_{1,38}=0.2$, $p>0.05$). When MDGs and TDRs were placed together on the birds back, depths were similar (paired t-test $t_6 = -0.6$, $p>0.05$).

Table 4.2: Proportion of time Shy Albatrosses spent sitting in or on the water (ie, when the TDR was wet) during their foraging trips in December 1994. Data are arranged for individuals as in Table 4.1.

	Daytime		Nighttime		
Time spent at sea (hours)	% of deployment time	% of daylight hours wet	% of deployment time	% of nightime hours wet	% of total time spent wet
18.5	62.2	0.5	37.8	0.8	0.6
45.1	68.9	9.5	31.1	3.3	7.6
58.9	76.2	8.8	23.8	2.7	7.3
60.9	65.5	1.0	34.5	0.0	0.7
32.1	78.2	14.9	21.8	3.4	12.4
63.1	66.7	4.3	33.3	4.6	4.4
79.7	64.9	23.9	35.1	46.0	31.6
69.4	69.7	1.2	30.3	3.1	1.8
65.3	67.9	4.2	32.1	3.4	3.9
43.3	67.6	4.5	32.4	14.6	7.8
86.7	67.7	8.2	32.3	23.6	13.2
53.0	73.6	3.0	26.4	11.6	5.3
37.5	62.7	3.4	37.3	13.4	7.1
30.6	77.2	5.3	22.9	10.0	6.3
26.2	73.3	7.3	26.8	11.4	8.4
Mean ± s.d.	69.5 ± 5.1	6.7 ± 6.1	30.5 ± 5.1	10.1 ± 11.8	7.9 ± 7.5

4.4 DISCUSSION

4.4.1 *Experimental Data*

As a MDG provides a single depth reading from all dives during a foraging trip the data must be cautiously interpreted. Simulations suggested that, as a mean, MDGs provide

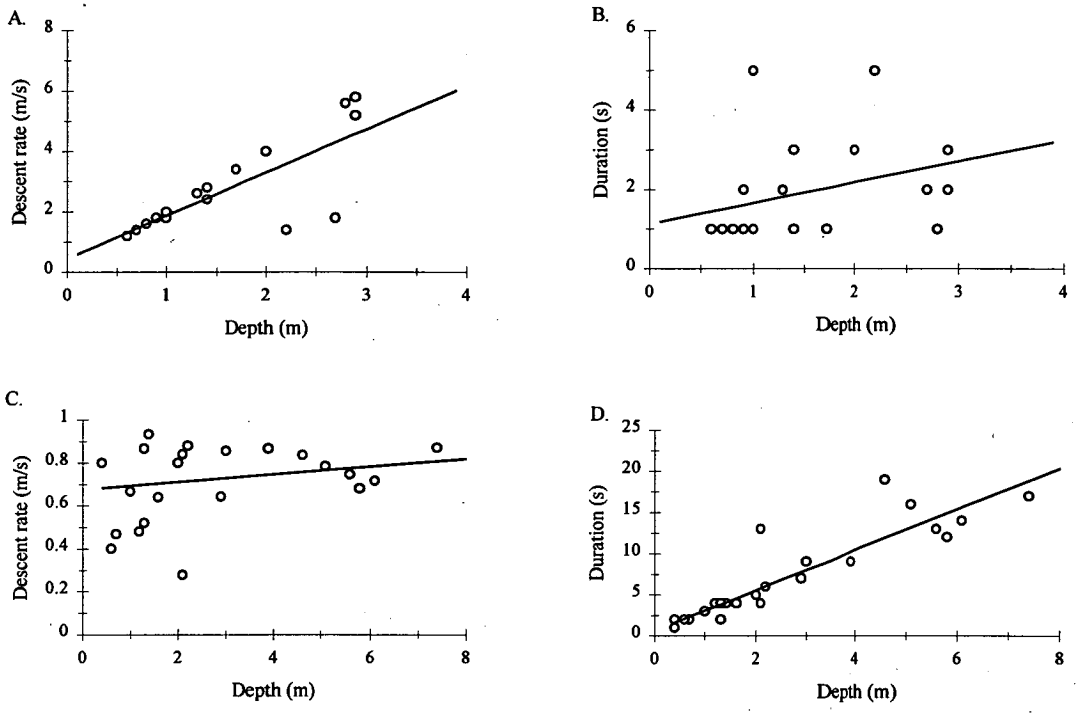

Figure 4.6: Shy Albatross plunge (A,B) and swimming dives (C,D) . Plunge Dives: (A) Relationship between dive depth and descent rate $Y=0.45 + 1.43$ (x), $r^2_{20}=0.63$, $F_{1,18}=31.3$, $p < 0.001$, and (B) dive depth and duration $Y=1.13 + 0.53$ (x), $r^2_{20}=0.11$, $F_{1,18}=2.3$, $p>0.05$ Swimming Dives: (C) Relationship between dive depth and descent rate $Y=0.67 + 0.02$ (x), $r^2_{32}=0.04$, $F_{1,30}=1.4$, $p>0.05$, and (D) dive depth and duration $Y=0.63 + 2.46$ (x), $r^2_{32}=0.84$, $F_{1,30}=159.4$, $p < 0.000$.

valuable information but that individual predictions may be highly inaccurate. MDGs may be particularly unsuitable for birds who dive frequently or for those which immerse for extended periods. MDGs are particularly prone to overestimating maximum depth when dives are shallow.

The experimental data were in broad agreement with those of Burger & Wilson (1988). Both studies found an increase in error with increasing diving frequency, and that varying the descent rate had little effect. However, one discrepancy concerned the effect of the cumulative dive time. Burger & Wilson (1988) reported that increasing dive duration had no effect on depth accuracy, however, their testing intervals ranged from just 0.5-8.0 minutes. With the more extended tests conducted in this study, it was clear that increasing dive times to one hour caused considerable overestimates. This would be a concern for albatrosses if gauges were leg-mounted, as the birds are known to spend considerable periods of time sitting on the water (Prince & Francis 1984). The effects of cumulative dive time would not be a concern for species such as albatrosses if gauges were back-mounted, but must be seriously considered for more aquatic species like penguins which spend extended periods of time underwater.

The TDRs performed accurately during the calibrations. With advances in technology the difficulties of measuring shallow depths should be overcome.

4.4.2 *Field Data*

4.4.2.1 *Maximum Depth Gauges*

Body placement significantly affected MDG accuracy, with gauges placed on the birds legs recording deeper dives than those placed on their back. Back-placed MDGs and TDRs recorded similar maximum dive depths. The deeper dives recorded by the leg-placed gauges may have resulted from birds spending considerable amounts of time sitting on the water, or from movements associated with their underwater swimming. It is important to consider the diving characteristics of a species prior to deploying MDGs, as these will likely indicate the magnitude of errors inherent in the data as well as guide decisions regarding the most appropriate attachment site.

4.4.2.2 *Time Depth Recorders*

This study has shown that Shy Albatrosses have a much greater diving capacity than was previously suspected. They can dive to at least 7 m and remain submerged for as long as 19 seconds. That 9 of the 15 birds dived indicates that diving forms a typical component of the foraging behaviour of this species.

The characteristics of plunge dives collected from the albatrosses correspond well with those of known plunge-diving seabirds such as gannets *Morus spp.* The mean dive duration of foraging gannets is 4 seconds (Duffy 1989), and birds are thought to reach between 2 and 4 m as a result of aerial plunging (Adams & Walter 1993). The plunge dives of the Albatrosses were similarly short (5 seconds or less), and birds reached a maximum depth of 2.9 m. In contrast, the swimming dives were significantly longer, had slower descent rates and penetrated deeper into the water column, confirming the suspicions of Prince et al. (1994) that albatrosses swim underwater.

There are apparent geographical differences in the diving behaviour of Shy Albatrosses. However, these differences may result from differences in the diet, sex (and hence body size), or breeding stage of the birds, as birds from Pedra Branca breed approximately 10-15 days later than those on Albatross Island. Such confounding factors are currently being explored.

Despite the fact that Shy Albatrosses dived only between dawn and dusk, they spent a considerable amount of time in contact with the water during both the day and night. Although diving is certainly indicative of foraging behaviour in these birds, the behaviours cannot be equated. The Albatrosses averaged less than two dives per day, strongly indicating that other techniques, probably surface seizing (Harper et al. 1985), also form an important feeding method for this species. It would be unlikely that such behaviour would be represented in their diving records.

The calculations of the proportion of time spent wet must be considered an absolute minimum. These calculations encompass only times when the bird's back was submerged adequately enough to activate the TDRs salt-water switch. Thus including periods when the birds were actively feeding underwater and times spent bathing. It would, however, be unlikely to include times when the birds were simply resting.

As the relatively proficient diving capabilities of albatrosses are recognized, they must be interpreted in light of implications for fisheries related mortality. Many of the world's

albatross populations are in decline (Weimerskirch & Jouventin 1987, Croxall et al. 1990), and deaths associated with longline fisheries have been identified as the major cause (Brothers 1991, Gales 1993). Albatrosses and other seabirds are vulnerable until baited hooks sink below their reach in the water column. Given the depths to which Shy Albatrosses can dive, and considering that their diving capabilities are inferior to those of the smaller albatrosses (Prince et al. 1994, N Brothers, unpubl. data.), we must recognize that albatrosses are susceptible to fishing practices for much longer than we previously believed. It is critical to continue monitoring albatross behaviour at sea to determine further how their habits place them at risk in the longline industry, and to interpret how these risks may be most appropriately minimized by effective design and deployment of mitigating measures.

4.5 ACKNOWLEDGMENTS

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Section B

Foraging Ecology

Chapter 5

ANNUAL COLONY ATTENDANCE PATTERNS OF TWO POPULATIONS OF SHY ALBATROSSES *Thalassarche cauta* BREEDING IN AUSTRALIA

5.1 INTRODUCTION

Breeding seabirds are typically central place foragers, with spatial separation of the breeding and feeding grounds. In Procellariiformes (albatrosses and petrels), the evolution of extreme life-history characteristics (delayed onset of maturity, single-egg clutches, slow chick growth, and long life expectancies) are thought to have developed in response to the vast distances between breeding and feeding grounds, and the general unpredictability of marine resources (Lack 1968, Ashmole 1971). However, even within the Procellariiformes there is a high degree of variability in life-history characteristics, which strongly link to the distribution of resources, and result in species-specific differences in foraging strategies (Weimerskirch et al. 1987).

The location of the foraging zone affects patterns of colony attendance during the breeding season and ultimately influences the life-history characteristics. Seabirds forage either in pelagic waters over the open ocean, in some cases focusing on specific frontal or bathymetric regions (e.g. Grey-headed albatrosses *Thalassarche chrysostomas* foraging in the Polar Frontal Zone, Prince et al. 1998), or in neritic waters over continental shelves and slope areas (e.g. Shy *Thalassarche cauta* and Black-browed *T. melanophris* albatrosses foraging 200-300 km from their colonies, Brothers et al. 1998, Chapters 3 & 8, Weimerskirch et al. 1997c, respectively). Within closely related taxa, pelagic species are more long-lived than neritic species, resulting in different decisions regarding current and future reproductive output (Weimerskirch et al. 1987). In particular, pelagic species are predicted to respond more strongly to deterioration in body condition during the breeding season (i.e., they are likely to abandon the attempt if body condition drops below threshold), as any single breeding attempt contributes relatively less to the lifetime reproductive output (Chaurand & Weimerskirch 1994a, Chastel et al. 1995a). In Wandering albatrosses *Diomedea exulans* and Blue petrels *Halobaena caerulea*, both pelagic species, body mass is strictly regulated during incubation and chick-rearing (Chastel et al. 1995a, 1995b, Chaurand & Weimerskirch 1994a, Weimerskirch 1995, Weimerskirch et al. 1997b). In neritic species such as Thin-billed prions *Patchyptila belcheri*, and Common Diving petrels *Pelecanoides urinatrix*, while body mass shows

both inter- and intra-annual variation, this does not correlate with reproductive success as it does for pelagic species (Chastel et al. 1995a). Neritic and pelagic species, then, respond differently to "poor" years, neritic species maintain breeding effort while pelagic species are either unwilling or incapable of similar maintenance.

Pelagic Procellariiformes are reported to adopt a two-fold foraging strategy when rearing chicks, undertaking both short and long foraging trips. Short foraging trips increase net energy flow to the chick, but this is at the expense of adult body condition, as adults have generally been found to lose mass on short trips (Weimerskirch et al. 1994, 1995 & 1997c). Long trips are undertaken when adults are in negative energy balance, and while food delivery to the chick is reduced, adults seem able to regain the mass lost on short trips (Weimerskirch et al. 1994, 1995 & 1997c). In contrast, while the body condition of neritic species such as the Black-browed albatross varies from one foraging trip to the next, the extent of the mass change does not influence either the duration of the subsequent trip to sea or the size of the meal next fed to the chick (Weimerskirch et al. 1997c). Body condition appears to play little role in regulating the provisioning strategy of this species (Weimerskirch et al. 1997c).

Shy albatrosses breed in the temperate waters surrounding Tasmania, Australia, in latitudes ranging from 40-44° South. They are neritic feeders, foraging in the continental shelf and shelf slope waters off southeast Australia during the breeding and non-breeding periods (Brothers et al. 1997, 1998, Chapters 3 & 8). Birds forage close to their colonies, and foraging trips and shifts at the nest are therefore relatively short throughout the breeding season. Unlike other albatross species, Shy albatrosses maintain a presence in the breeding colonies almost year-round. The broad aim of this study was to quantify year-round colony attendance patterns for two of the Tasmanian Shy albatross populations, incorporating both inter- and intra-annual variation, along with assessing any differences between the genders or breeding sites. Concurrent studies of at-sea distribution allowed changes in the duration of foraging trips to be interpreted with respect to changes in foraging location. Finally, concurrent deployment of automatic weighing platforms (Chapter 7) enabled detailed, long-term collection of adult body masses at various times of the year, as well as during and between shifts at the nest. The influence of body mass and rates of body mass change were studied to elucidate their influence on subsequent foraging behaviours.

5.2 METHODS

5.2.1 *Species and study sites*

Recent revisions to albatross taxonomy have elevated the Shy albatross populations breeding in Tasmania to full species status (Nunn et al. 1996, Robertson & Nunn 1998). Two of these populations were studied; Albatross Island (40° 24'S, 144° 32'E) in western Bass Strait from 1995/96 to 1997/98, and Pedra Branca (43° 52'S, 146° 58'E) off the south coast of Tasmania in 1997/98. Breeding is annual, and while the first eggs are laid late August, most are laid in September (N. Brothers, unpubl. data). Eggs are incubated at Albatross Island for 73 ± 1.0 days (range 71-77, n=62; N. Brothers unpubl. data), in alternating shifts by both parents. Chicks hatch between late November and mid-December and are brooded by both parents over the next 3-4 weeks. After leaving the chick alone at the nest, parents forage simultaneously for food and return to the colony only briefly over the next 14-16 weeks to feed their chick. The earliest chicks leave the colony late March, and fledging continues throughout April (Figure 5.1). After fledging, chicks are absent from the natal colony for at least two years (N. Brothers, unpubl. data). Adults depart the colony for a brief period after the chicks have fledged, and then return to spend much of the winter, non-breeding period attending the colony.

5.2.2 *Data collection*

Colony attendance patterns of the albatrosses were collected remotely at both sites using a combination of VHF transmitters (Sitrack Ltd., Havelock North, New Zealand) and remote telemetry recording systems (ATS, Advanced Telemetry Systems, Isanti, MN, USA). To minimize size and bulk, transmitters were packaged with an internal loop antennae and their range was approximately 150 m. The transmitters alone weighed 16 g and after being sewn into padded Velcro bands, secured with quick setting epoxy, the final package weighed between 20 and 21 g (45.5 mm high x 23.0 mm wide x 38.9 mm long, 0.4-0.6% adult body mass). Transmitters were placed upon birds (on the right leg) as they were incubating or brooding their chick (Figure 5.2, Table 5.1). Whenever possible, both members of each breeding pair were studied at Albatross Island. However, to reduce disturbance at Pedra Branca, transmitters were placed upon single incubating birds during a brief visit to the Island in November 1997. Study birds were banded with a stainless-steel band on the left leg and colour-marked on the breast (with Dulux Hi Gloss enamel spray paint) for identification from a distance.

In the first season (1995/96) transmitters pulsed at 30 ppm, yielding a maximum life of

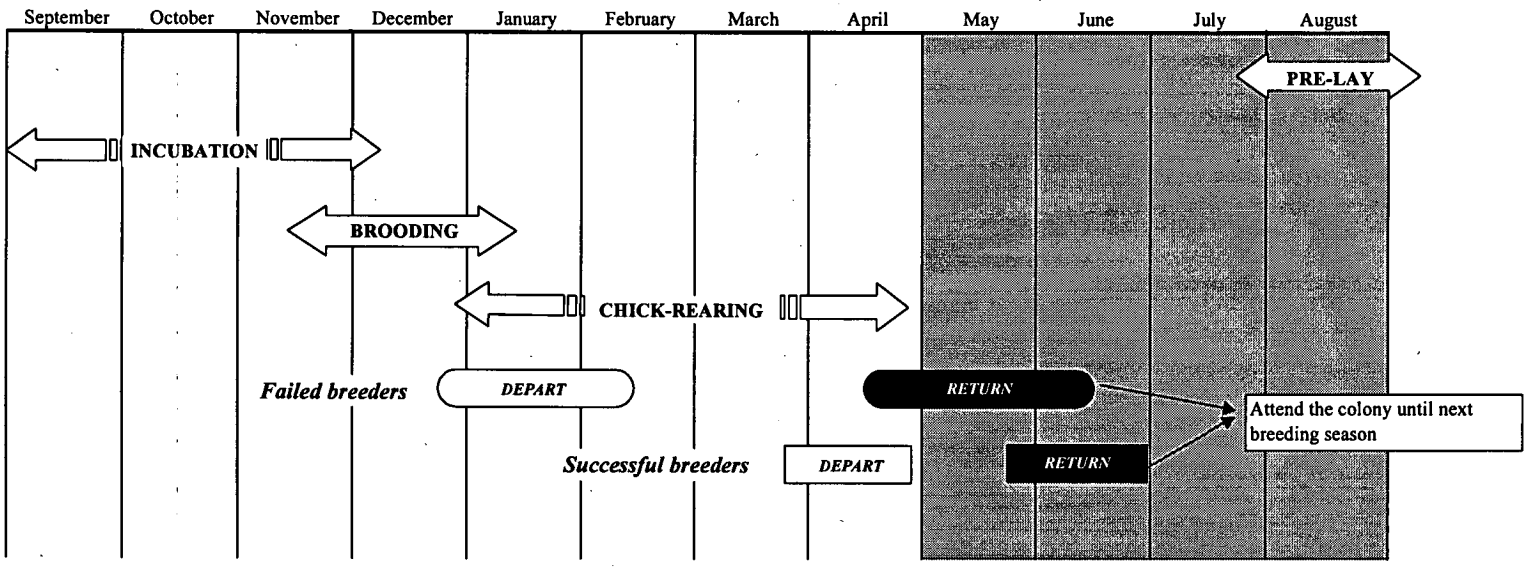


Figure 5.1: Schematic of the major breeding and non-breeding activities of Shy albatrosses throughout their annual cycle. The non-breeding period is shaded grey.

Figure 5.2: Adult Shy albatross from Albatross Island brooding an approximately 3 week old chick. Note the VHF transmitter on its right leg.

9.4 months. Subsequently using a "long-life" option, and the same pulse rate, the transmitters lasted for 12.7 months, allowing birds to be studied for the entire breeding and post-breeding periods. To avoid disturbance to adults during the breeding period, their sex was determined the following winter, using morphometric measurements (Hedd et al. 1998, and Chapter 2). Transmitters were also then removed and re-powered for the next breeding season.

Table 5.1: Details of the numbers of transmitters deployed at Albatross Island and Pedra Branca, and their deployment schedules between 1995/96 & 1997/98. The number of transmitters placed upon breeding pairs is given in brackets with the balance being placed upon single birds.

Breeding site	Season	Total transmitters	Number deployed during incubation	Number deployed during chick-brooding
Albatross Is.	1995/96	21	21 (20)	6 (6)
Albatross Is.	1996/97	28	28 (28)	0
Albatross Is.	1997/98	27	27 (26)	0
Pedra Branca	1997/98	10	10 (0)	0

A concurrent parental provisioning study at Albatross Island (Chapter 7), aimed to longitudinally study the provisioning performance of five breeding pairs across three years. Four of the original five pairs were studied in all years (R45, Z7, I3 and R35), but breeding failures resulted in partial records for two of the four pairs in two separate years (I3 and R35, Table 5.2). The final original pair (Z6) was studied only during the first two years, and it's replacement (Z10) only in the last two years (Table 5.2). Eight additional attendance only pairs were studied in 1995/96, eight in 1996/97 and nine in 1997/98. During the first two years of the study, when nest failure occurred during incubation or chick-brood, transmitters were removed and placed upon other pairs of birds breeding at the time. However, during the final year, transmitters were left upon failed breeders to examine their patterns of colony attendance and to provide insight into the influence of breeding demand on presence in the colony.

Three of the five pairs initially chosen (R35, R45 and I3) were known to have had at least one previous successful breeding attempt, and at least one member of each pair was of known age. The remaining pairs were selected randomly throughout the colony. While some subsequently chosen nests contained known-age birds, nothing was known of the breeding history.

Table 5.2: Details of the pairs of the birds studied in two or more years. The outcome of each breeding attempt (presence or absence of a fledgling) is indicated. Adult ages (as in 1995/96) are indicated when known, with age being assigned from the fledging year (f=female, m=male).

	1995/96		1996/97		1997/98	
Nest (Age in 1995/96)	egg	fledgling	egg	fledgling	egg	fledgling
R45 (f=14)	√	√	√	√	√	√
Z7	√	√	√	√	√	√
I3 (f=13, m=10)	√	√	√	√	√	x
R35 (f=14, m=11+)	√	√	√	x	√	x
Z6	√	√	√	x	not monitored	
Z10	not monitored		√	√	√	x

In each year, 2-4 week field trips were conducted to Albatross Island during incubation (September/October), chick-brood (December/January), mid-chick-rearing (February) and fledging (April), and a description of the nest contents was noted at these times (i.e., egg, live chick, dead chick or empty nest). A trip was also made to Albatross Island during July or August each year (in the nonbreeding period). When breeding failures occurred between nest checks at Albatross Island (prior to the end of chick brood) failure dates were assumed to coincide with the first time both members of the pair were absent from the colony. Post-brooding failure dates were assumed to coincide with the last adult presence in the colony for the season.

At Pedra Branca, it was not possible to regularly check the study nests, and day trips to the Island were conducted only in November/December 1997 and May 1998. Intermittent operation of the ATS system resulted in data being collected only between 9 November-11 December 1997, and between 19 March-29 April 1998. Knowledge of the attendance patterns of birds from Albatross Island was used to interpret changes with breeding stage at Pedra Branca. Prior to 11 December, regular presence in the colony was taken to indicate that pairs were still breeding, while sporadic attendance indicated nest failure (as birds are incubating or brooding at that time of year). Further, if adults regularly attended the colony during March and April they were assumed to have bred successfully, while if they were not recorded during this period their breeding attempt was assumed to have failed.

At Albatross Island, body masses were collected remotely for five pairs of adults using automatic weighing platforms (Francis Scientific Instruments, Cambridge, UK). Adult mass (± 10g) was recorded at 10 minute intervals in 1995/96, but at 30 minute intervals in 1996/97 and 1997/98 to increase the duration of the records. As the albatrosses added

nest material over the bowls, the platforms required taring and re-calibrating whenever the risk of adult disturbance was minimal. Nests were calibrated prior to egg laying (July/August), at the end of the brooding period (December/January), and again at fledging in April, after the chick had departed. Adult weights were subsequently corrected for materials added to the nest platforms as well as for the nest contents (i.e., the egg or chick). As the addition of materials to the nests, particularly during incubation shifts, sometimes caused uncertainties it was not always possible to extract absolute masses. In such instances, just the relative mass changes between foraging trips were noted.

5.2.3 *Sampling protocols*

Both memory limitations of the telemetry system and behavioural changes of the birds during the breeding season required temporal changes in the sampling protocols. During incubation and chick-brooding, when shifts at the nest were generally 24 hours or more, colony presence/absence was recorded electronically by the ATS at least once per hour (but once every two hours at Albatross Island in 1997/98 to extend the recording period). After leaving chicks alone at the nest, parents visit the colony only briefly to feed, sometimes departing in less than five minutes. During this stage presence/absence was recorded continually, and with 28 transmitters, this equated to a cycle time of approximately 4.5 minutes. Despite the relative brevity of adult visits, the probability of recording their presence was actually quite high. Using three years of automatic nest data, and making the assumption that all meals received by chicks were delivered by their parents, just 1% (12 of 1,226) of the adult visits were missed. In these instances birds presumably spent less than the 4.5 minutes required to be detected in the colony.

5.2.4 *Data analysis*

5.2.4.1 *Attendance and foraging patterns*

For purposes of analysis, the breeding season was divided into five stages, and the non-breeding season into two. The breeding season included early incubation (September-November), late incubation (November/December), chick-brooding (December/January), early chick-rearing (January) and late chick rearing (February-April). The breeding timetable is somewhat asynchronous, with egg-laying spanning approximately 30 days (late August to late September), and this resulted in a range of dates for the stages indicated above (Figure 5.1). Early and late incubation were distinct as, similar to other albatross species (Croxall 1984, Weimerskirch et al. 1993), Shy albatross foraging trip

and shift durations at the nest decrease in the days prior to hatching. A distinction was also made between early and late chick-rearing as the duration of foraging trips in the first 30 days post-brood (early chick-rearing) were shorter and less variable than those observed later in the season (late chick-rearing).

The non-breeding period included 1) the over-winter period, which encompassed the time from the post-breeding return to the month prior to egg-laying (late April-late July), and 2) the pre-laying period, which encompassed the remaining time until eggs were laid (August/September; Figure 5.1).

The duration of both adult foraging trips and shifts at the nest were calculated to the end of chick-brood. The duration of foraging trips was calculated from the time of the birds departure from the colony until its subsequent return, while the duration of shifts at the nest were the inverse, calculated from a birds arrival in the colony until its subsequent departure. At certain times of the year, most notably during early incubation, arrivals to the colony were not always accompanied by shift changes at the nest; i.e., birds did not always swap duties. Nest changeovers are dependent on the intentions of the sitting bird, not the bird off the nest, and as a result, arriving birds could often spend extended periods of time sitting either by their mates or near the edge of the colony, before they again headed out to sea. Shift durations were not calculated during such visits. As adults return to the colony only to feed chicks after the end of brood, just the duration of foraging trips were calculated in the later chick-rearing phases.

Arrival times were examined throughout the breeding season relative to ambient light conditions. Each day was broken into four periods; daytime, nighttime and morning and evening twilight. Morning twilight commenced with the beginning of nautical twilight (defined as the instant when the centre of the sun is at a depression angle of 12° below the horizon) and ended with sunrise, while the evening twilight period commenced with sunset, and continued until the sun was at a depression angle of 12° below the horizon. Daytime incorporated the period from sunrise to sunset and nighttime, the period from the end of nautical twilight in the evening to the beginning of nautical twilight the following morning.

Laying and hatching dates were not precisely known. Hatching dates were estimated from the size of the chick on arrival to the colony in conjunction with the date its parents shifts at the nest decreased to 24 hours. Hatching was observed for a single pair, and shift durations decreased to 24 hours on the hatching day. Laying dates were back-calculated from hatching dates, using a standardized incubation period of 73 days (N. Brothers,

unpubl. data). Chick-brood was considered over when the chick was first left alone in the colony. The duration of the fledging (or chick-rearing) period was calculated from hatching to the day the chick departed its nest. Fledging was assumed to coincide with nest departure, and not colony departure, as chicks can spend days within or on the outskirts of the colony prior to leaving the island, but the duration of this period has not been quantified.

5.2.4.2 *Research questions*

The major research questions and the statistical approaches used to answer them are outlined below. Because data for the members of breeding pairs are not independent, analyses were conducted using the 'nest' as the replicate unit rather than the individual birds. Mean values for foraging trip and shift durations were calculated for each bird in each breeding stage, and indices relating to the performance of the pair were compiled.

1) Is there a sex difference in foraging trip or shift durations at the nest during the breeding season?

2) Do foraging trip or shift durations at the nest vary with breeding stage?

Prior to answering the first question it was necessary to determine if the behaviour of males and females changed in a similar manner across the breeding season. This was assessed using a repeated measures analysis of variance (ANOVA) on gender difference scores (mean of the males score - mean of the females score) in each breeding stage. This condition satisfied, one-sample (paired) t-tests were used to evaluate whether the sexes actually differed (mean gender differences across all stages were evaluated against the null hypothesis that the mean difference was 0). Changes in foraging trip or shift durations at the nest throughout the breeding season (question 2), were also assessed using repeated measures ANOVAs on the nest means ((mean males score + mean females score)/2). A series of planned comparisons (profile contrasts) were used to assess where any differences lay. To ensure statistical independence, the above analyses were run separately for each year.

3) Do foraging trip or shift durations at the nest vary between years?

While inter-annual comparisons would have been most appropriately conducted using two-way repeated measures ANOVAs, gaps in the data from both transmitter and breeding failures left inadequate numbers of replicates. Differences were therefore assessed on a stage by stage basis, using a series of one-way ANOVAs, with birds studied

longitudinally included only in their first year. To guard against the increased possibility of making a Type 1 error, the p value for each comparison was decreased to 0.01. Seasonal change also was assessed separately for the pairs studied longitudinally using two-way repeated measures ANOVAs.

4) Are foraging trip or shift durations at the nest similar for successful and failed breeders?

The foraging performance of failed and successful breeders was compared in two ways. First, the groups were compared in the stage where the failure occurred (using nest means). The second approach involved a retrospective examination of the foraging performance of late-failing birds (i.e. pairs which raised their chick past brooding) to see if poor performances earlier in the season were implicated in later failures. Comparisons were made with independent samples t-tests (or Mann-Whitney U tests) for the stage by stage comparisons, and two-way repeated measures ANOVAs when data were analyzed retrospectively.

5) Are foraging trip or shift durations at the nest similar at the two breeding sites, Albatross Island and Pedra Branca?

Comparisons between breeding sites were possible only to the end of chick brooding and only in 1997/98, when data were collected contemporaneously at both sites. Two-way repeated measures ANOVAs were conducted on nest means with breeding site as the between subjects factor.

With the exception of question 4 in which the performance of failed and successful breeders was compared, analyses were conducted using only successful pairs. Whenever more than two groups of data were analysed with one-way repeated measures ANOVAs (in violation of the sphericity assumption), the multivariate Wilk's lambda statistic was used to assess significance of the results (Zar 1996). When the multivariate approach was not possible, Huynh-Feldt adjusted (H-F adj.) probability values were used.

5.2.4.3 *Body mass*

Adult body masses were collected during 4 periods (winter (May-July), pre-laying (August-September), incubation (September-November) and chick-brooding (December/January)), averaged, and presented according to time of year. The mass of each individual upon arrival to and departure from the colony was noted for each foraging trip. During the non-breeding period (winter and pre-laying) as well as during incubation

birds spend extended periods of time sitting on the nests. In such instances, overall and proportionate rates of mass loss were calculated. The mass gained (or lost) at sea between successive shifts on the nest was also calculated. These data were used to explore relationships between:

1) proportionate and overall rates of mass loss by males and females during incubation shifts;

2) the duration of incubation foraging trips and the mass gained (or lost) at sea;

3) the influence of departure mass and total mass lost during an incubating shift on the subsequent foraging trip duration;

4) the influence of departure mass on the mass gained at sea;

5) the relationship between the mass lost while incubating and the amount gained prior to return to the colony (both absolute and relative);

6) proportionate and overall rates of mass loss during the incubation and non-breeding periods.

Daily changes in body mass were also used to construct upper and lower limits for the resting metabolic rates of Shy albatrosses, and these were compared with theoretical estimates based upon classic relationships with body mass.

Expected basal and existence metabolic rates were estimated from the standard relationships defined by Kendeigh et al. (1977). Basal metabolic rate (BMR)=$0.5224W^{0.7347}$, and existence metabolic rate (EMR)=$4.142W^{0.5444}$ for non-passerine birds, where metabolic rate is in kcal/day and W is body mass in kg (Kendeigh et al. 1977). Body masses used in these calculations were those obtained 48 hours after the bird's arrival in the colony, and they were assumed to represent the post-absorptive state.

Metabolic rates were also estimated from the observed patterns of mass loss. The accuracy of such estimates is largely dependent upon a knowledge of the composition, and hence the energy equivalent, of the lost material (Groscolas 1988). As the composition of the mass loss by Shy albatrosses in this study was unknown, upper and lower metabolic estimates were constructed using composition data obtained from the literature for fasting (non-moulting) seabirds. An upper boundary was constructed using values from Emperor penguins *Aptendoytes foresteri*, where 61.7% of the mass lost

during phase II fasting resulted from utilization of fat, 5.9% from protein, with water comprising the remainder. Data from two species that normally fast for short periods (and rely less heavily on fat stores) were used to calculate a range for the lower boundary. 30.1%, and 10.8% of the mass lost by Gentoo penguins *Pygoscelis papua* resulted from utilization of fat and protein respectively (Cherel et al. 1993), while comparable values for Wilson's storm petrel *Oceanites oceanicus* were 36% and 17% (Groscolas et al. 1991). Water comprised the remainder of the mass loss for both species. The energy equivalents of fat and protein were taken as 39.7 and 16.7 kJ/g, respectively (Petrusewicz & Macfayden 1970). Analyses were conducted using Spearman rank regression analysis or Mann-Whitney U tests, as appropriate.

Analyses were conducted in Statistica (release 4.5, StatSoft Inc.), and values are presented as means ± 1 S.D.

5.3 RESULTS

5.3.1 *General description of the data*

Between 1995/96 and 1997/98, attendance data were obtained for 24 pairs of birds that raised their chick to fledging at Albatross Island, and for five birds that raised a chick at Pedra Branca (Table 5.3). Physical obstruction of the signals at Pedra Branca resulted in intermittent data collection, leaving just eight study nests at that site. Further, intermittent problems with the telemetry system itself resulted in two periods of data collection (9 November-11 December 1997, and 19 March-29 April 1998).

The overall breeding success (chicks fledged from eggs laid) of birds carrying VHF transmitters on Albatross Island was higher than that observed in the study colony as a whole, during each year (Table 5.3). Of the 18 pairs that failed on Albatross Island, seven did so during early incubation, three failed during chick-brood, three failed early in chick-rearing and the five remaining pairs failed during late chick-rearing. On Pedra Branca, two pairs failed during incubation, and the other pair failed post-brood. Breeding success counts at Pedra Branca in 1997/98 were conducted too late to allow comparison with success rates in the colony as a whole.

On Albatross Island 19 of the study birds were of known age, having been banded on the Island as chicks. There was no effect of maternal age ($t=0.90$, $df=14$, $p=0.19$, successful females 14 ± 1.29 years vs unsuccessful females 13 ± 2.69 years), or of overall age (males and females combined) on breeding success ($t=1.32$, $df=24$, $p=0.20$, 13.5 ± 1.88

vs. 12.1 ± 2.85 years), with failed and successful breeders being of similar age (Figure 5.3). However, the sample size was small, and the mean age of both groups was similar; 7-8 years above the age at first breeding (N. Brothers unpubl. data). There were also small numbers of young birds and no older birds (>16 years) in the sample.

Table 5.3: Details of the number of Shy albatross nests studied during each season and at each site, along with a comparison of the overall breeding success at study nests to that observed in the colony as a whole.

Breeding site	Season	Number of nests studied	Number producing a fledgling (%)	Overall colony breeding success
Albatross Is.	1995/96	13	8 (62%)	16%
Albatross Is.	1996/97	14	10 (71%)	51%
Albatross Is.	1997/98	14	6 (43%)	36%
Pedra Branca	1997/98	10	5 (50%)	Unknown

Birds were largely diurnally active in the colony (Figures 5.4 & 5.5). Of 5,003 arrivals to Albatross Island, 96.5% (4,828) occurred either during daylight (82.4%) or during the morning (10.8%) or evening (3.3%) nautical twilight periods, with only 3.5% of all arrivals occurring at night (Figure 5.4). The pattern was similar between years, stages of the breeding season, and the sexes (Figure 5.5). The diurnal pattern was similar at Pedra Branca; of 243 arrivals recorded, 97.0% (235) occurred during daylight (90.0%) or during the morning (4.1%) and evening (2.9%) twilight periods, with just 2.9% of all arrivals occurring at night. Arrivals were also not equally probable during each daylight hour at either site (Figure 5.4, χ^2=1425.6, df=18, $p < 0.0001$, χ^2=54.1, df=16, $p < 0.0001$, respectively). At Albatross Island arrivals peaked early in the morning and again late in the evening, while at Pedra Branca, a strong morning activity peak was followed by generally consistent numbers of arrivals each hour for the remainder of the day.

5.3.2 *Colony attendance patterns during the breeding season*

5.3.2.1 *Albatross Island*

5.3.2.1.1 Successful pairs

During the three breeding seasons, the duration of 3,361 foraging trips and 1,137 shifts at the nest were calculated for successful pairs of Shy albatrosses (Appendices 5A and 5B). Because of the high degree of inter- and intra-individual variability, data were presented

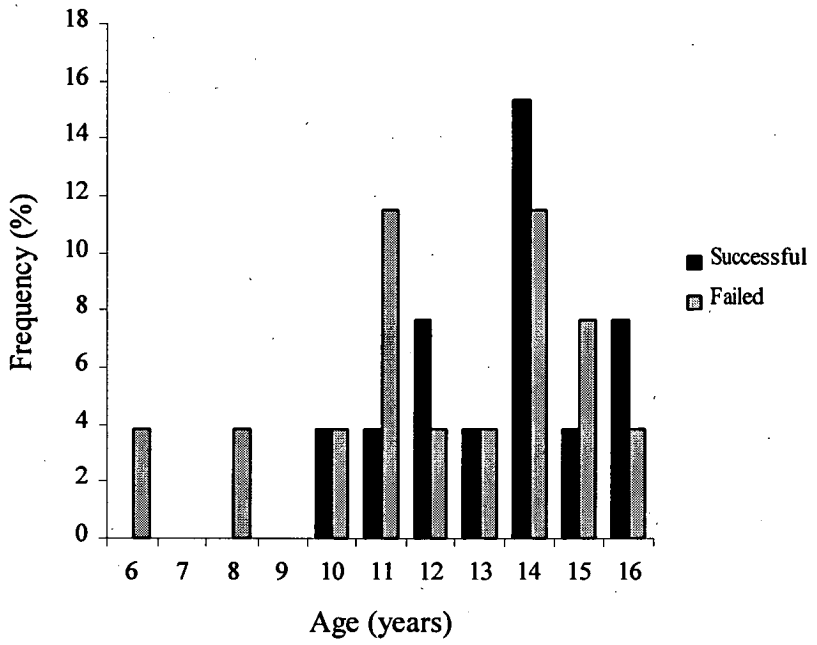


Figure 5.3: Histogram of the ages of known age successful and failed breeders.

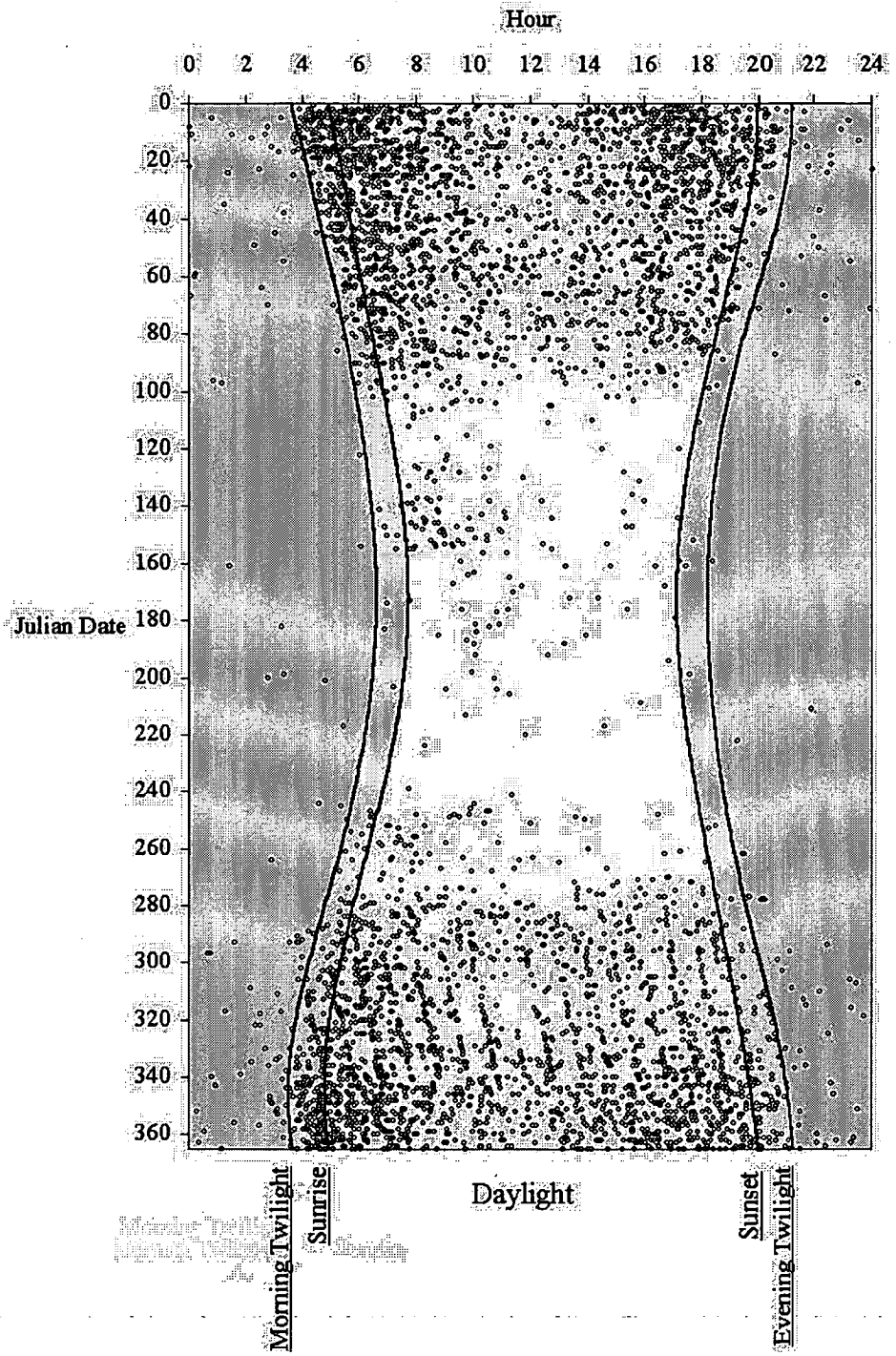


Figure 5.4: Time of Shy albatross arrivals to Albatross Island relative to changes in ambient light conditions throughout the year. Nighttime is shaded dark grey, the twilight periods a lighter grey, while daylight remains clear. Data were pooled across years.

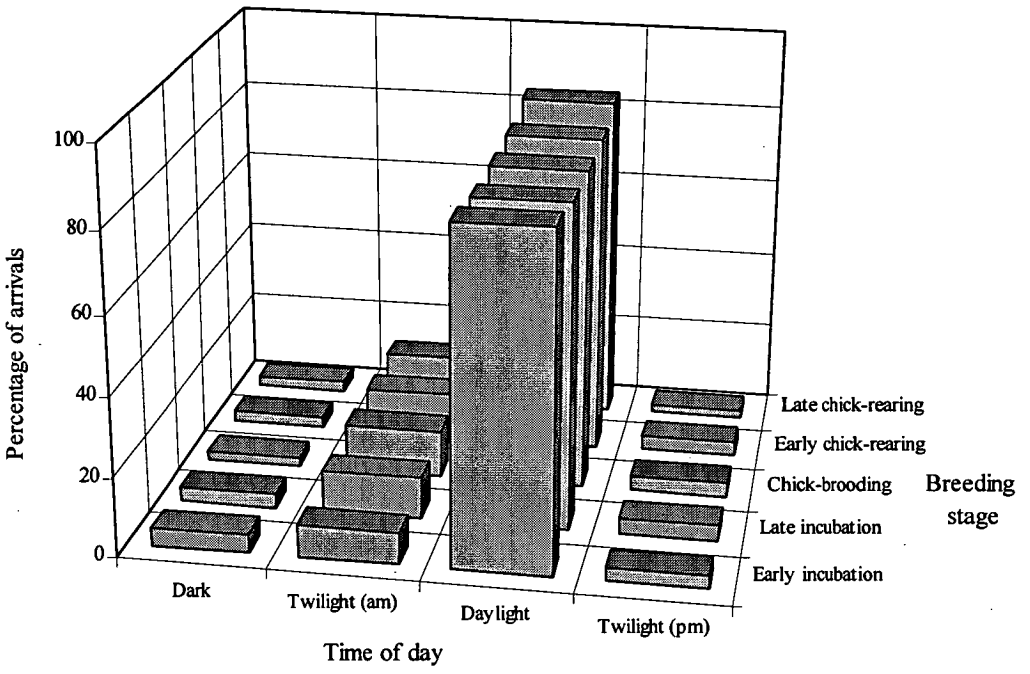


Figure 5.5: Proportion of Shy albatross arrivals to Albatross Island relative to ambient light conditions broken down according to stage of the breeding season.

as the mean ± 1 S.D. for each individual in each breeding stage. There is some discrepancy in the duration of foraging trips and shifts at the nest during incubation and chick-brooding (Appendices 5A and 5B, and Figure 5.6), with shifts at the nest tending to last longer. This resulted from the propensity of the albatrosses to refuse shift changes at the nest when their partners returned from foraging trips; changeovers being refused on 149 of 1,258 (11.8%) arrivals. Birds were more likely to refuse shift changes early in the season (χ^2=61.1, df=2, $p < 0.01$), with changeovers refused on 21.1% of arrivals during early incubation, as opposed to just 15% and 4.9% of arrivals during late incubation and brooding, respectively. There was no sex bias in this tendency, with equal proportions of males and females refusing to swap duties in each breeding stage (χ^2=2.6, df=2, $p > 0.05$, χ^2=3.4, df=2, $p > 0.05$, χ^2=0.8, df=2, $p > 0.05$, respectively for early and late incubation and chick-brooding).

5.3.2.1.2 Gender effects

Differences between the genders in foraging trip and shift duration at the nest were similar across breeding stages in all years (1995/96 foraging trips Wilk's Lambda $F_{1,4}$=0.47, p=0.78, shift durations $F_{2,8}$=2.62, H-F adj p=0.13; 1996/97 foraging trips Wilk's Lambda $F_{3,4}$=3.29, p=0.18, shift durations $F_{2,18}$=1.10, H-F adj p=0.35; 1997/98 foraging trips $F_{4,12}$=1.00, H-F adj p=0.44, shift durations $F_{2,10}$=0.81, H-F adj p=0.47). There were no sex differences in foraging trip or shift durations at the nest in any year ($p > 0.20$ for all). However, it is worth examining trends in the overall nest difference scores with data pooled across years (Table 5.4). Scores for foraging trips tended to be negative both early and late in the season, indicating that females tended to spent longer at sea than males. During chick-brood and early chick-rearing, however, difference scores were close to zero, indicating that the sexes were behaving similarly (Table 5.4). The trend was reversed for shift durations at the nest; these tended to be positive early in incubation, indicating that males spent longer on the nest than females (0.2 ± 0.79 days, n=17).

With the obvious exception of egg-laying, there was no indication that either sex was more likely to be in attendance at any particular point during the breeding season. Equal numbers of males and females were present at the nest on the estimated hatching day (χ^2=0.8, df=1, $p > 0.05$, n=20), and the sexes were also equally likely to first leave the chick unattended (χ^2=0.04, df=1, $p > 0.05$, n=23).

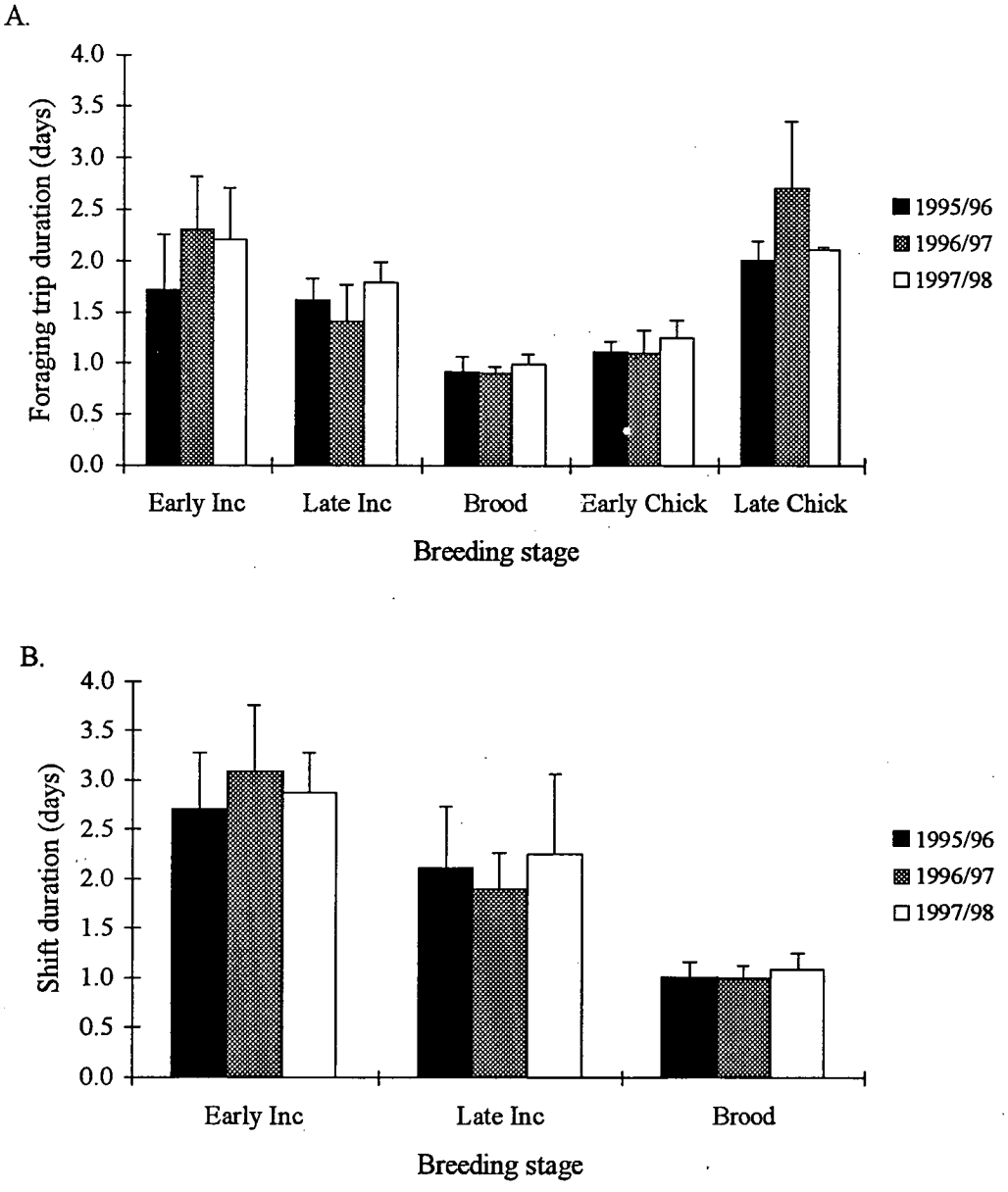


Figure 5.6: Duration of (A) foraging trips and (B) shifts at the nest during each breeding stage and season for Shy albatrosses at Albatross Island.

Table 5.4: Mean nest difference scores (mean male score - mean female score) and mean foraging trip durations for male and female Shy albatrosses across the five breeding stages. Data for all years are combined, and presented in days.

Breeding stage	n	Nest difference scores mean ± sd	95% confidence limits	Male foraging trip duration mean ± sd	Female foraging trip duration mean ± sd
Early incubation	16	-0.4 ± 0.84	-0.83, 0.06	2.1 ± 0.67	2.3 ± 0.53
Late incubation	16	-0.1 ± 0.76	-0.52, 0.29	1.8 ± 0.55	1.7 ± 0.48
Chick-brooding	18	0.0 ± 0.22	-0.13, 0.09	1.0 ± 0.16	0.9 ± 0.05
Early chick-rearing	15	0.1 ± 0.29	-0.10, 0.22	1.3 ± 0.16	1.1 ± 0.15
Late chick-rearing	12	-0.3 ± 1.12	-1.00, 0.43	2.2 ± 0.39	1.9 ± 0.31

5.3.2.1.3 Intra-annual effects

Foraging trip durations varied across breeding stages in all years (Figure 5.6a; 1995/96, $F_{4,16}$=15.27, H-F adj $p < 0.001$; 1996/97, $F_{4,24}$=27.87, H-F adj $p < 0.0001$; 1997/98, $F_{4,12}$=15.31, H-F adj $p < 0.01$), but there were subtle differences between years in the timing of these differences. In 1996/97 all adjacent breeding stages were significantly different ($p < 0.05$ for all), but in both 1995/96 and 1997/98, foraging trips were of similar duration during early and late incubation, and again during chick-brood and early chick rearing ($p > 0.05$ for all contrasts). The duration of shifts at the nest also varied across the breeding season in all years (Figure 5.6b; 1995/96, $F_{2,8}$=29.29, H-F adj $p < 0.001$; 1996/97 $F_{2,18}$=66.09, H-F adj $p< 0.001$; 1997/98, $F_{2,10}$=21.39, H-F adj $p < 0.001$), progressively decreasing from early incubation to hatching. In 1995/96 and 1996/97 all adjacent breeding stages were significantly different ($p < 0.05$ for all), whereas in 1997/98 shift durations at the nest decreased from late incubation to chick-brood ($p < 0.05$), but were similar in duration during early and late incubation ($p=0.11$).

Shy albatross foraging trips were equally long early and late in the breeding season (averaging 1.5-3 days), when birds were incubating and rearing large chicks. Foraging trips and shifts at the nest were shortest (averaging just 24 hours) after the chicks hatched and remained similarly short in the month after chicks were first left alone at the nest. Chicks were brooded for 27.3 ± 3.86 days (range 21-36 days, n=27) and variance in the duration of foraging trips and shifts at the nest was low during this stage (Appendix 5A and Figure 5.6). The total duration of the fledging period was 127 ± 7.4 days (n=10).

5.3.2.1.4 Inter-annual effects

There were no differences between years in foraging trip or shift durations at the nest ($p > 0.01$ for all comparisons). Only during late chick-rearing was there any indication of a change between years, with foraging trips tending to be longer in 1996/97, but not significantly so ($F_{2,11}=5.53$, $p=0.022$; nest mean 2.8 ± 0.70 days, versus 2.0 ± 0.19, and 2.1 ± 0.01 days in 1995/6 and 1997/98, respectively).

When only longitudinally studied pairs (I3, R45 and Z7) were assessed, there was again some indication of a change between years, with longer foraging trips in 1997/98 (Figure 5.7). Pairs at nests R45 and Z7 fledged their chicks in all three seasons, but the pair at I3 lost their chick late in February 1998. Across all breeding stages there were no inter-annual effects ($F_{2,3}=3.48$, $p=0.17$), but excluding late chick-rearing, foraging trips tended to be longer in 1997/98 than in 1995/96 ($F_{2,4}=9.04$, $p < 0.05$; Tukey's HSD, $p < 0.05$). Shift durations at the nest were similar between years ($F_{2,4}=0.47$, $p=0.66$).

5.3.2.1.5 One parent chicks

At four successful nests, a single parent was responsible for feeding the chick during some or all of the post-brood chick-rearing period (Appendix 5A). Two of the desertions were by males, and two by females, one of each sex in 1995/96 and 1996/97. The number of visits made by single parents to their chicks was compared with one-half the number of visits made by birds feeding along with their mate. In 1995/96 the number of visits made by single and coupled parents was similar ($\chi^2=1.40$, df=1, $p > 0.05$), indicating that in this year, single parents did not or could not alter their provisioning schedules. However, these chicks fledged none the less. In 1996/97, food deliveries by single parents were substantially greater than half the deliveries made by pairs ($\chi^2=96.9$, df=1, $p < 0.001$). Further, two of these pairs (R45 and I3) were studied longitudinally, and in all but one season, both the male and female fed the chick to fledging. When feeding alone, these parents were able to significantly increase the number of feeds delivered to the chick ($\chi^2=16.9$, df=2, $p < 0.05$). This particularly resulted from the increased provisioning rate of the female at nest R45, when she delivered 64 meals, an average increase of 66% over the same period in 1995/96 (40 meals) and 1997/98 (37 meals) when she was feeding along with her mate. The meals were 19% larger, but more significantly, they were delivered at almost double the rate.

Given the differential provisioning of male and female chicks (Chapter 7) it would be interesting to examine whether the response of single parents differed depending on the sex of the chick they were raising. The sex of chicks raised by single parents in 1995/96

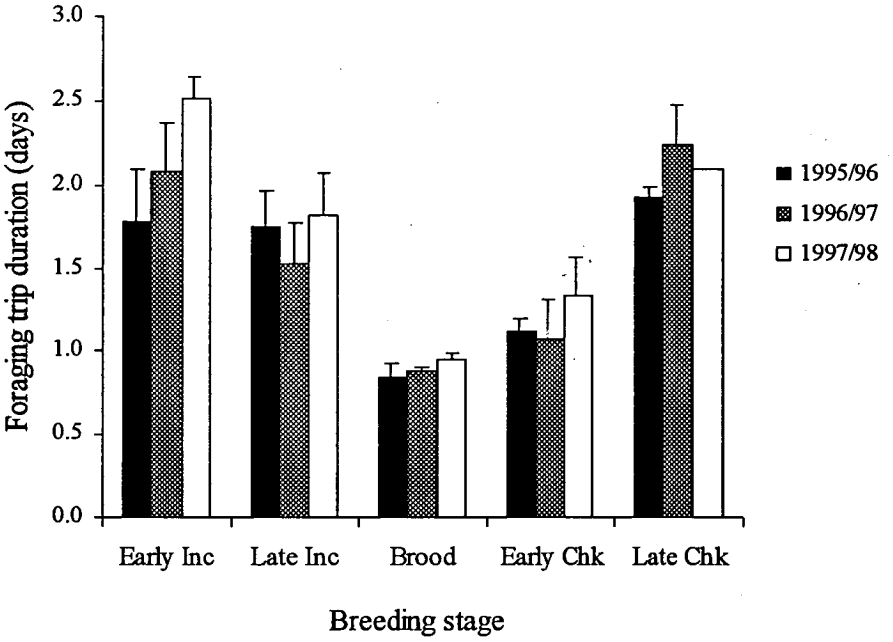


Figure 5.7: Duration of foraging trips for the longitudinally studied pairs of Shy albatrosses from Albatross Island between 1995/96 to 1997/98.

was unknown, but in 1996/97 the chick at nest R45 was male and the chick at nest I3 was female. It is interesting that when feeding alone, provisioning rates to the male chick were increased, while those to the female chick were unaltered. However, there is no way of knowing whether this was mediated by different chick responses, or differential parental quality.

5.3.2.1.6 Failed breeders

For each individual failed breeder, the mean duration of foraging trips and shifts at the nest are given in Appendices C and D, respectively, for the breeding stages up to and including the stage where the failure occurred. While breeding, the duration of 1,155 foraging trips and 516 shifts at the nest were determined.

Failed breeders also exhibited a propensity to refuse shift changes at the nest. This tendency varied through time (χ^2=23.6, df=2, $p < 0.05$), being strongest early in incubation (29.5% of arrivals met with refusal), and becoming less so when chicks were brooded (10.6% of arrivals met with refusal). There was no sex bias in the tendency, with similar proportions of refusals made by males and females (χ^2=2.72, df=1, $p > 0.05$). However, the overall proportion of arrivals without nest changeovers (142 of 653, 21.7%) was higher for failed than successful breeders (paired t-test, t=-8.16, df=2, $p < 0.05$), perhaps indicating that nest relief routines were less well coordinated in the unsuccessful pairs.

Given no significant inter-annual effects, failed breeders were pooled across years and their foraging performances compared with successful breeders. Failed breeders were grouped according to the stage when they failed, and stage by stage comparisons were conducted. In the stage where the failure occurred, foraging trip durations were similar for failed and successful breeders ($p > 0.15$ for all). The same was true for the duration of shifts at the nest (p=0.16). The only difference between these groups was in the duration of shifts at the nest during chick brood. Pairs which failed during brood spent longer on the nest than pairs that were successful (1.6 ± 0.51 vs. 1.0 ± 0.16 days, Mann-Whitney U test, U=7.50, $p < 0.05$).

Looking retrospectively, there was a tendency for late failing pairs to have spent significantly longer on the nest early in the breeding season than successful pairs (two-way repeated measures ANOVA; $F_{1,26}$=3.66, p=0.066, Figure 5.8). Sex difference scores for the failed breeders were close to zero (-0.1 ± 0.78 vs. -0.4 ± 0.84, t=-1.07, df=30,

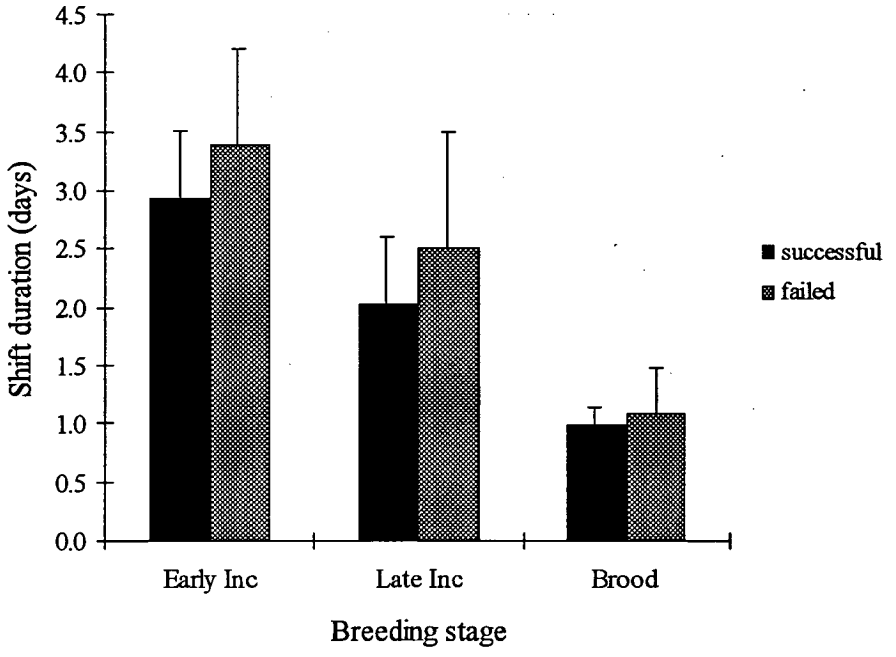


Figure 5.8: Comparison of the duration of shifts at the nest for successful and failed pairs of Shy albatrosses from Albatross Island between 1995/96 and 1997/98.

p=0.29; and -0.1 ± 0.87 vs. 0.2 ± 0.79, t=0.88, df=31, p=0.39, respectively) indicating that for pairs that failed during chick-rearing, investment was shared more equally by the sexes early in the breeding season, with failing females investing relatively more.

Estimated laying dates ranged between 4-29 September. There was no indication that laying date influenced the outcome of the breeding attempt, with similar proportions of early (birds laying in the first half of the period) and late (those laying in the second half) laying birds fledging chicks (χ^2=0.17, df=1, p > 0.05, n=27). To determine if major deviations in laying date (either early or late) influenced breeding success, outcomes were also compared for birds laying within and outside one standard deviation of the mean laying date (20 September ± 6 days). Again there was no effect, with similar proportions successful in each group (χ^2=1.54, df=1, p > 0.05). It should be noted, however, that since the laying date was backcalculated from the hatching date, data for pairs (n=7) that failed during incubation could not be included. While there was no indication that these pairs differed from later failing pairs, we have no way of quantifying the potential bias.

5.3.2.2 *Pedra Branca*

5.3.2.2.1 Successful pairs

During 1997/98 foraging trip durations of Shy albatrosses breeding on Pedra Branca were calculated for 177 trips to sea, as were the durations of 68 shifts at the nest for successful pairs of birds. Because of the high degree of variability within and between birds, data were again presented separately for each individual (Appendix 5E). To be comparable with data for Albatross Island (i.e., means of nest means), data are presented only for the first three stages of the season. Both foraging trip and shift durations at the nest were longest during early incubation, averaging almost three days (Figures 5.9a and 5.9b) and shortest (averaging just 24 hours) when chicks were brooded. During late chick-rearing, birds returned every 1.7 ± 0.51 days (n=5 birds) to feed chicks.

Foraging trip durations decreased progressively from early incubation to brooding ($F_{2,6}$=10.43, H-F adj p=0.016), with brooding trips being significantly shorter than those late in incubation (p=0.060; Figure 5.9a). Shift durations at the nest decreased across breeding stages (Figure 5.9b), but the trend was not statistically significant ($F_{2,4}$=5.94, H-F adj p=0.135).

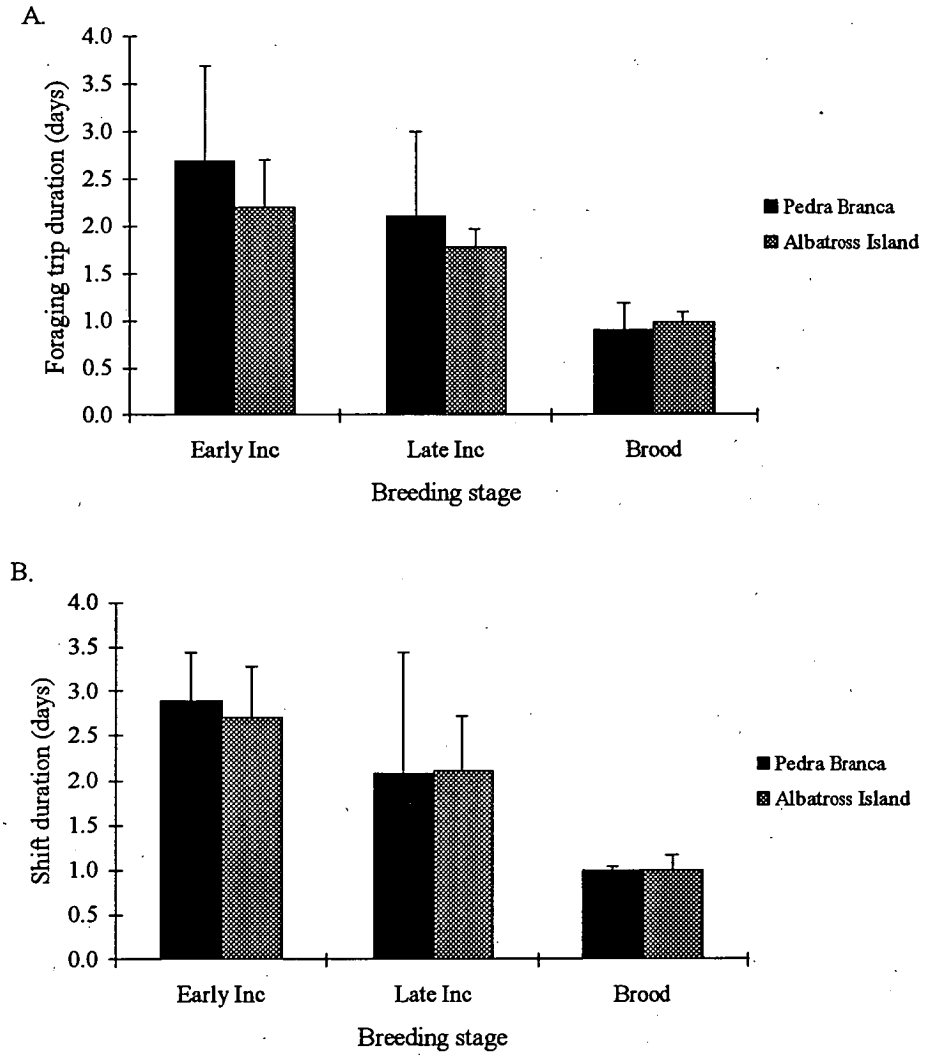


Figure 5.9: Comparison of the duration of (A) foraging trips and (B) shifts at the nest for Shy albatrosses breeding at Albatross Island and Pedra Branca in the 1997/98 breeding season.

5.3.2.2.2 Failed breeders

The foraging behaviour of failed and successful breeders could be compared only in early incubation, and foraging trips were of similar duration between groups ($t=0.29$, $df=3$, $p=0.79$).

5.3.2.3 *Comparison between breeding sites*

The duration of foraging trips and shifts at the nest were similar at Albatross Island and Pedra Branca during 1997/98 (Figure 5.9a and 5.9b; $F_{1,8}=0.52$, $p=0.493$, $F_{1,7}=0.01$, $p=0.919$, respectively).

5.3.3 *Colony departure and post-breeding absence*

5.3.3.1 *Albatross Island*

The fledging period of Shy albatrosses is 127 ± 7.4 days (range 112-136 days, n=10). The majority of successful parents for which departure dates were known (22 of 34, 65%) vacated the colony for the season prior to their chick's departure. Eleven parents (32%) made one additional visit to the colony in the week after the chick had left, and three parents (9%) made a second such visit. Successful adults and their chicks, then, depart the colony for the season almost simultaneously at the end of the rearing period.

Attendance patterns of failed breeders were studied during 1997/98 (and for one bird in 1995/96). Birds which lost their eggs or small chicks regularly attended the colony until late December or mid-January. This coincides with the time that successful breeders are nearing the end of chick-brood. The longest time a failed breeder attended the colony was 92 days (male at nest A1 in 1995/96). This bird lost his egg on 8 November 1995 and regularly attended the colony until 7 February 1996 (Table 5.5). When failing during early or late chick-rearing, adults departed for the season within days. Table 5.5 provides details of post-breeding departure dates for birds in relation to breeding outcomes.

The duration of the post-breeding absence is known for 25 birds. Return date and the duration of the post-breeding absence are both strongly influenced by the outcome of the previous breeding attempt. Because of their earlier departures from the colony, failed breeders spent significantly longer periods at sea than successful breeders (111 ± 14.0 vs. 65 ± 18.5 days, $t=-7.19$, $df=23$, $p < 0.001$). Adults which failed the previous season also returned to the colony significantly earlier ($t=2.94$, $df=23$, $p < 0.01$). Successful breeders

began returning to the colony 10 May, with birds arriving through to 18 June (mean arrival 27 May ± 14.4 days, Table 5.5). Failed breeders began returning 16 April (while chicks were still fledging) and new arrivals continued until 3 June (mean arrival 10 May ± 15.5 days). Return dates were known for both members of 6 breeding pairs (Table 5.5). For all six pairs, males returned to the colony before females, arriving on average 10 ± 9.2 days (range 2 - 25 days) earlier. Irregardless of their sex or the outcome of their previous breeding attempt, however, all birds returned well in advance of the next breeding season, with even the latest returning bird reaching the colony 18 June, some 10 weeks before eggs are laid.

Table 5.5: Post-breeding departures and duration of colony absence following the 1995/96 and 1997/98 breeding seasons at Albatross Island. Breeding outcomes (successful or not) are indicated. For failing birds, the failing stage is indicated (st 1=early incubation; st 2=late incubation; st 3=brooding; st 4=early chick-rearing; st 5=late chick-rearing).

Season	Nest	Sex	Breeding outcome	Departure date	Return date	Post-breeding absence (days)
1995/96	I3	F	Successful	24 March	18 June	86
	I3	M	Successful	14 April	02 June	49
	Z3	F*	Successful	20 February	23 May	94
	R1	M	Successful	09 April	04 June	56
	R45	M	Successful	31 March	23 May	53
	Z5	F	Successful	02 April	02 June	61
	Z6	F	Successful	29 March	05 June	68
	Z6	M*	Successful	28 February	03 June	96
	Z7	M	Successful	12 April	28 May	46
	A1	M	Failed (st 1)	07 February	07 May	90
	R21	F	Failed (st 5)	17 February	03 June	119
	R21	M*	Failed (st 5)	06 February	31 May	115
	Z4	F	Failed (st 4)	21 January	16 April	86
1997/98	V5	F	Successful	07 March	10 May	65
	Z7	M	Successful	05 April	24 May	49
	Z13 new	F	Successful	09 April	24 May	45
	I8	M	Failed (st 1)	02 January	17 May	134
	Next Z9	F	Failed (st 5)	24 January	22 May	118
	Next Z9	M	Failed (st 5)	23 January	07 May	104
	V3	M	Failed (st 4)	29 January	22 May	112
	V7	F	Failed (st 3)	26 December	02 May	126
	V7	M	Failed (st 3)	08 January	29 April	111
	V13	F	Failed (st 5)	19 January	16 May	117
	V13	M	Failed (st 4)	15 January	21 April	96
	Z10	M	Failed (st 1)	22 December	22 April	121
			Successful breeders (± SD)		27 May ± 14.4 d	64 ± 18.5 d
			Failed breeders (± SD)		10 May ± 15.5 d	111 ± 14.0 d

*indicates early nest desertion

5.3.3.1.1 Over-winter attendance at the colony

Patterns of winter attendance at the colony were collected for 13 birds following the 1995/96 season, and for 12 birds following the 1997/98 season (Table 5.6). After returning, birds maintained a regular presence in the colony until they next bred. The longest period spent away from the colony subsequent to the winter return was 14.8 days. Although variable, foraging trip durations tended to decrease and the time birds spent attending the colony per "shift" tended to increase as the next breeding season approached (Spearman's $R=-0.216$, $p < 0.01$, $n=161$ and $R=+0.346$, $p < 0.0001$, $n=173$, respectively). Unfortunately, data were never collected for the entire nonbreeding period. In the portions studied, birds spent as much as 53% of their time in the colony, but 10-30% was more typical (Table 5.6). In the month prior to egg-laying in 1997, males spent slightly more time in the colony than females (paired t-test, $t=2.42$, $df=4$, $p=0.072$; $67 \pm 8.8\%$ vs $46 \pm 11.5\%$; $n=5$ nests). This sex difference was also reflected in the winter data set as a whole, with males spending twice as much time in the colony as females ($30 \pm 17.3\%$ vs $15 \pm 12.1\%$, for males and females, respectively, $t=2.34$, $df=18$, $p < 0.05$).

5.3.4 *Body mass*

5.3.4.1 *Variation in body mass through the year*

As body mass data were not collected during all periods for all individuals, or for all individuals in all years, data were pooled across years. In the five longitudinally studied pairs, mean male body mass was greater than female body mass throughout the year (paired t-tests, arrival mass $t=5.74$, $df=3$, $p < 0.05$, departure mass $t=4.11$, $df=3$, $p < 0.05$; Table 5.7). The female at nest R35 was heavier than her mate during the pre-egg stage in 1996/97, but the trend reversed after the egg was laid. In all other pairs males outweighed females throughout the season. Body mass, however, was not constant through time (Table 5.7). As there was insufficient data to run repeated measures ANOVAs, adjacent time periods were compared using a series of paired t-tests on mean data. For both males and females, body mass was similar from the over-winter return through incubation ($p > 0.05$ for all), but it decreased between incubation and the end of chick-brood (males, $t=-5.55$, $p < 0.05$; females $t=-4.16$, $p=0.053$). An example of this body mass change for the pair at nest Z7 during 1996/97 is given in Figure 5.10. No data were available for the female during the return period.

Table 5.6: Over-winter colony attendance patterns of Shy albatrosses following the 1995/96 and 1997/98 seasons. When attendance records spanned less than 10 days the percentage of total time spent in the colony was not calculated.

Season	Nest	Sex	Return date	Duration of records (days)	Foraging trip duration (days)	Periods spent in colony (days)	% time in the colony
1995/96	A1	M	07 May	111.8	3.5 ± 3.60 (24)	1.1 ± 1.33 (23)	24%
	I3	F	18 June	18.0	6.7 ± 2.92 (2)	2.3 ± 1.32 (2)	26%
	I3	M	02 June	1.0	0.6 (1)	0.4 (1)	-
	R1	M	04 June	5.1	0.5 ± 0.10 (2)	2.0 ± 2.78 (2)	-
	R21	F	03 June	45.8	4.4 ± 4.74 (9)	0.7 ± 0.62 (9)	14%
	R21	M	01 June	12.8	3.9 ± 3.81 (3)	0.3 ± 0.36 (3)	7%
	R45	M	23 May	22.2	3.1 ± 1.63 (4)	2.9 ± 1.90 (4)	53%
	Z3	F	23 May	15.0	6.8 ± 3.18 (2)	0.7 ± 0.10 (2)	10%
	Z4	F	16 April	104.6	4.0 ± 4.00 (19)	1.5 ± 2.16 (20)	29%
	Z5	F	02 June	66.3	4.5 ± 2.46 (10)	2.1 ± 1.94 (10)	32%
	Z6	F	05 June	87.0	3.7 ± 1.98 (18)	1.1 ± 1.45 (18)	23%
	Z6	M	03 June	3.4	1.0 (1)	2.0 (1)	-
	Z7	M	28 May	88.9	2.1 ± 2.25 (20)	2.4 ± 2.54 (20)	53%
1997/98	V5	F	10 May	23.6	4.6 ± 3.29 (6)	0.1 ± 0.12 (7)	2%
	Z7	M	24 May	9.6	1.2 ± 0.59 (2)	2.2 ± 1.63 (3)	-
	Z13 new	F	24 May	9.7	6.9 (1)	0.6 ± 0.71 (2)	-
	I8	M	17 May	16.6	1.7 ± 1.38 (4)	1.5 ± 2.24 (5)	45%
	Next Z9	F	22 May	10.5	-	0.04 (1)	1%
	Next Z9	M	07 May	26.7	5.5 ± 4.15 (4)	0.8 ± 0.85 (6)	17%
	V3	M	22 May	10.4	3.1 ± 3.57 (2)	1.6 ± 1.37 (3)	45%
	V7	F	02 May	31.8	7.6 ± 6.09 (4)	0.2 ± 0.21 (6)	2%
	V7	M	29 April	34.6	4.3 ± 2.97 (6)	1.2 ± 0.89 (7)	24%
	V13	F	16 May	17.4	2.7 ± 3.31 (4)	0.2 ± 0.13 (6)	6%
	V13	M	21 April	42.3	3.0 ± 2.78 (9)	0.9 ± 0.89 (10)	22%
	Z10	M	22 April	41.7	3.5 ± 2.91 (10)	0.4 ± 0.60 (11)	11%

Table 5.7: Mean body mass of male and female Shy albatrosses (kg) throughout the year. Data were collected using automatic weighing platforms, and presented as means ± 1 SD, with the number of birds in parentheses

Sex	Point of time	Over-winter return	Pre-laying	Incubation	Chick-brood ((near end)
Male	Arrival	4.7 ± 0.37 (7)	4.7 ± 0.22 (4)	5.1 ± 0.30 (5)	4.6 ± 0.07 (4)
	Departure	4.4 ± 0.39 (6)	4.2 ± 0.27 (4)	4.5 ± 0.44 (5)	4.1 ± 0.16 (4)
Female	Arrival	4.0 ± 0.34 (4)	4.4 ± 0.30 (4)	4.6 ± 0.36 (5)	4.1 ± 0.18 (4)
	Departure	4.1 ± 0.28 (3)	4.1 ± 0.37 (4)	4.2 ± 0.36 (5)	3.6 ± 0.18 (5)

5.3.5 *Mass loss during shifts on the nest*

Instantaneous mass loss rates were calculated for incubating birds at 12-hourly intervals to determine the duration of digestion of the stomach contents (Figure 5.11). The proportion of mass lost decreased significantly during the first 36 hours on the nest, but

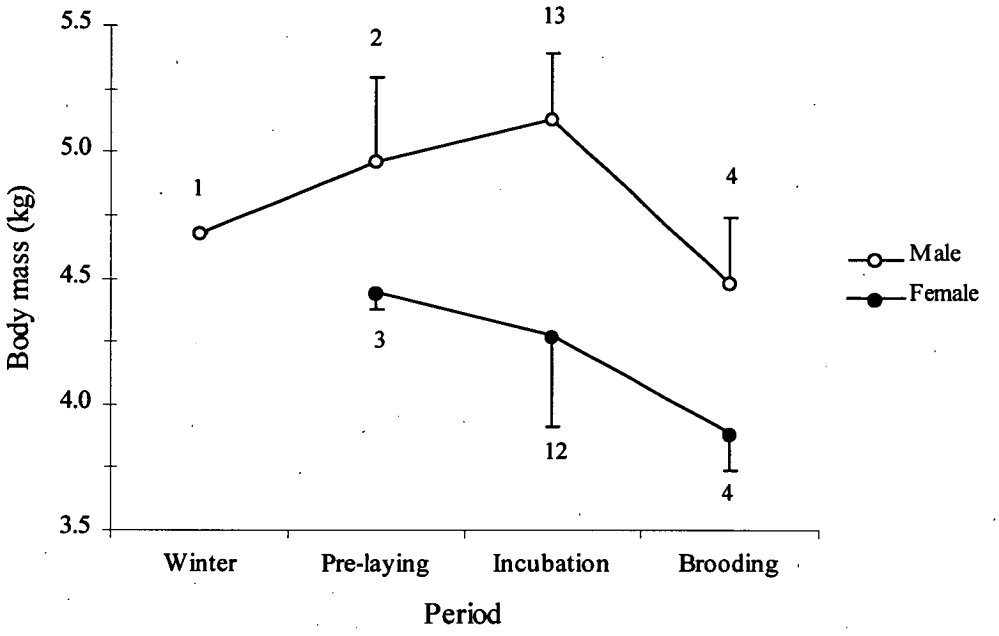


Figure 5.10: Mean (±1 S.D.) body mass of the male and female at nest Z7 prior to and during the 1997/98 breeding season. The number of shifts upon which the means are based are indicated.

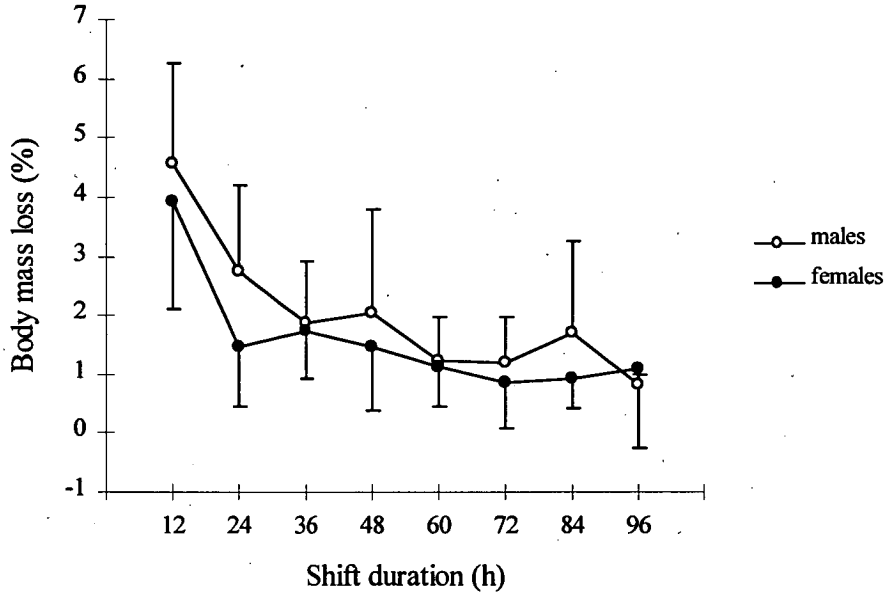


Figure 5.11: Proportion of initial body mass lost by male and female Shy albatrosses at 12-hourly intervals during their incubation shifts. The proportion decreased significantly to 36 hours, but remained constant thereafter.

showed no significant decrease thereafter (Spearman rank, R=-0.58, n=114, $p < 0.0001$, R=-0.17, n=89, p=0.106). To minimize the effect of digestion of the stomach contents and initial voiding of liquids, calculations of weight loss during shifts on the nest were restricted to shifts lasting a minimum of two days.

Figure 5.12 provides an example of a typical weight loss curve from an incubating male during October 1997. Shy albatrosses lose an average of 12 ± 6.2% (n=42) of their initial body mass during each incubation shift. In one extreme case, a male abandoned the egg when his body mass decreased by 43%, after having spent 32 days on the nest. During the course of a normal duration incubation shift, Shy albatrosses lose approximately 200 g or 4% of initial mass per day. Both the overall and proportionate daily mass loss rates were similar for males and females (Table 5.8; Mann-Whitney U=235, df=1, p=0.564, and Mann-Whitney U=211, df=1, p=0.969). After sitting on the nest for 48 hours (i.e., after the stomach contents had presumably been digested and voided) there was a significant decrease in both overall and proportionate rates of mass loss per day (Table 5.8; Mann-Whitney U=840, df=1, $p < 0.001$, Mann-Whitney U=830, df=1, $p < 0.001$). Birds then lost an average of 112 g or 2.2% of initial body mass each day, with rates again similar for males and females (Table 5.8; Mann-Whitney U=70, df=1, p=0.445, Mann-Whitney U=69, df=1, p=0.546).

Mass loss rates were also calculated for birds sitting on the artificial nests during the winter, non-breeding period. Non-breeding birds departed the colony after losing 11 ± 4.3% (n=35) of initial mass, a proportion similar to that lost during each incubation shift (Mann-Whitney U=829, df=1, p=0.336). Across full shifts during the non-breeding period birds lost 162 g or 3.5% of their initial body mass per day, and these rates were significantly lower than those observed during incubation (Table 5.8, Mann-Whitney U=991, df=1, $p < 0.01$ Mann-Whitney U=939, df=1, $p < 0.05$, respectively). Rates of mass loss were again halved after digestion of the stomach contents, with birds losing, on average, 78 g or 1.7% of their initial body mass per day. While lower, these rates were not significantly different than those observed during incubation (Mann-Whitney U=307, df=1, p=0.114, and Mann-Whitney U=297, df=1, p=0.179, for overall and proportionate rates, respectively).

5.3.5.1 *Predicted and estimated metabolic rates*

Estimates of the basal and existence metabolic rates of Shy albatrosses during incubation and the non-breeding periods are given in Table 5.9. Estimates of metabolic rate based upon observed rates of mass loss were constructed for shifts lasting a minimum of two

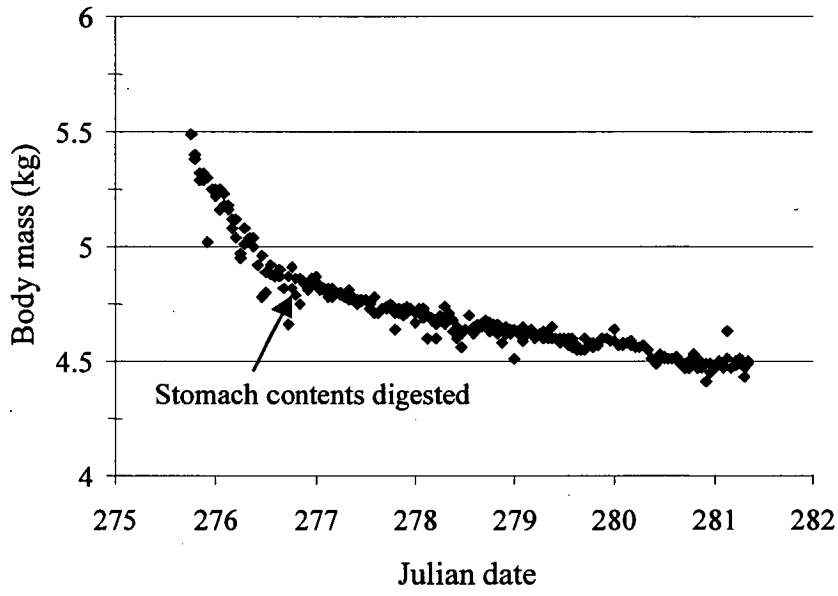


Figure 5.12: Body mass decline of a male Shy albatross across a 5.5 day incubation shift in October 1997. The point at which the stomach contents were digested is indicated by an arrow.

Table 5.8: Descriptions of the duration of Shy albatross incubation shifts and foraging trips along with associated changes in body mass. Rates of mass loss were calculated for shifts lasting a minimum of 2 days. Measures are provided as the mean ± 1 SD with the range of values beneath.

	Males	Females	Pooled	Gender difference
Incubation shift duration (days)	4.2 ± 5.84 (25) 2.0-32.0	2.8 ± 0.84 (17) 2.0-5.1	2.9 ± 0.74 (375)* 1.7-3.9	ns
Mass at start of incubation shift (g)	5148 ± 375 (25) 4350-5930	4761 ± 355 (17) 4260-5230	4991 ± 411 (42) 4260-5930	Mann-Whitney U=323.5, $p < 0.01$
Mass when returned to sea (g)	4460 ± 511 (25) 2890-5350	4269 ± 349 (17) 3790-4740	4381 ± 457 (42) 2890-5350	ns
Daily mass lost on the nest (g/day) over the full shift	208 ± 83.8 (25) 69-457	184 ± 54.6 (17) 95-324	198 ± 73.5 (42) 69-457	ns
Proportional daily mass lost (%/day) over the full shift	4.0 ± 1.56 (25) 1.4-9.0	3.9 ± 1.08 (17) 2.2-6.1	4.0 ± 1.37 (42) 1.4-9.0	ns
Daily mass lost on the nest (g/day) from 2 days onward	115 ± 61.3 (17) 52-277	103 ± 90.3 (7) 5-223	112 ± 69.1 (24) 5-277	ns
Proportional daily mass lost (%/day) from 2 days onward	2.2 ± 1.17 (17) 1.0-5.5	2.2 ± 1.91 (7) 1.0-5.0	2.2 ± 1.38 (24) 0.1-5.5	ns
Foraging trip duration (days)	2.0 ± 0.83 (35) 0.7-5.1	2.6 ± 1.00 (32) 0.5-5.0	2.1 ± 0.74 (455)* 0.9-3.8	ns
Mass gain at sea (g)	516 ± 287 (35) -330-940	290 ± 301 (32) -280-1320	408 ± 313 (67) -330-1320	Mann-Whitney U=833, $p < 0.001$
Daily mass gain at sea (g/day)	294 ± 206 (35) -184-738	140 ± 166 (32) -108-721	220 ± 202 (67) -184-738	Mann-Whitney U=821, $p < 0.001$
Proportional daily mass gain at sea (%/day)	7.3 ± 4.39 (30) 0.2-17.4	3.6 ± 4.04 (28) -2.0-16.0	5.5 ± 4.58 (58) -2.0-17.4	Mann-Whitney U=633, $p < 0.001$

*Average of individual bird means, and individual ranges

and a half days, and were based upon the rates of mass loss following two days of fasting (i.e., when post-absorptive) until the bird departed the colony.

Table 5.9: Estimates of the metabolic rate (MR) of Shy albatrosses derived using theoretical equations as well as when based upon rates of body mass loss. Estimates from rates of mass loss were made from 2 days into the shift until the bird subsequently returned to sea.

Time[1]	Sex	n	Average mass (at 48 h)	Mass loss (g/kg/day)	Mass loss (g/day)	Calculated MR (kJ/day) Lower[2]	Upper	Theoretical MR (kJ/day) BMR	EMR
Inc	M	17	4,502	25.5	115	1,581 1,970	2,930	1,057	1,690
Inc	F	7	4,320	23.8	103	1,416 1,764	2,624	1,026	1,654
Non-br	M & F	20	4,258	18.3	78	1,073 1,336	1,987	1,014	1,640

[1] Inc=Incubation, and Non-br=Non-breeding period
[2] Upper value in each cell based upon mass loss composition data from Gentoo penguins, and bottom value from Wilson's storm petrel.

The degree of correspondence between theoretical metabolic rate estimates and those constructed from rates of body mass loss depended upon assumptions regarding the composition of the lost material (Table 5.9). For example, the upper boundaries, constructed using composition data from fasting Emperor penguins, were substantially higher than EMR estimates throughout the study. However, the lower boundary values, based upon data from fasting Gentoo penguins, were closer to theoretical expectations and fell between BMR and EMR during both incubation and the non-breeding (winter) periods. It is also worth noting that metabolic estimates based upon rates of mass loss during winter were more in line with theoretical predictions than those from incubation. In fact, while predictions averaged 45% greater than BMR during incubation, they lay just 6% above BMR in winter. Irrespective of the seasonal difference, though, it seems likely that during normal fasts, Shy albatrosses utilize relatively little fat, and this perhaps accounts for as little as 30% of the mass lost.

5.3.5.2 *Mass gain at sea between Incubation Shifts*

Males and females spent similar periods at sea early in incubation, but overall males gained more mass than females, and they also gained proportionately more mass per foraging day (Table 5.8; Mann-Whitney U=833, df=1, p=0.001, and Mann-Whitney U=633.0, df=1, p=0.001, respectively). Figure 5.13 is a histogram depicting the distribution of the mass changes for males and females. Males gained mass on all except one of 35 trips to sea during incubation, whereas on five of 32 trips females either just maintained mass (one trip) or lost mass (four trips).

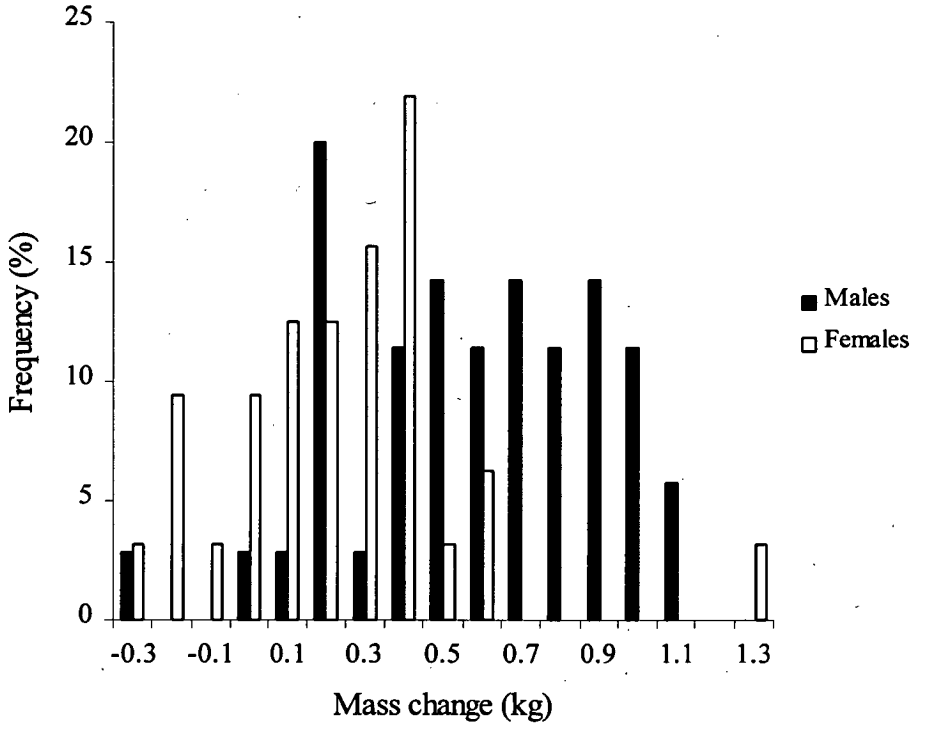


Figure 5.13. Histogram of the changes in body mass between incubation shifts for male (n=35) and female (n=32) Shy albatrosses at Albatross Island, Tasmania.

5.3.5.3 *Relationships between foraging parameters and mass changes during incubation*

Individual albatrosses tended to maintain or to increase in mass from pre-laying to incubation (Table 5.7). Overall, the duration of an incubation shift influenced the duration of the subsequent foraging trip to sea, and this tendency was stronger for females than males (Spearman's R=0.270, p=0.0004, and R=0.155, p=0.04, respectively, Figure 5.14a). Interestingly, when examined for the smaller subset of birds for which there was contemporaneous mass data, neither the mass of the bird at the end of it's incubation shift (departure mass) nor the total mass lost during the shift influenced the subsequent foraging trip duration, for either sex ($p > 0.05$ for all, Figures 5.14b and 5.14c). For males, the departure mass was negatively related to the mass change at sea (Spearman's R=-0.442, p=0.02), indicating that males which were lighter leaving the nest tended to regain more mass before returning, but this was not so for females (Figure 5.14d). Overall, the extent of the body mass change at sea was unrelated to the duration of the foraging trip, or to the extent of mass loss on the nest (Figures 5.14e and 5.14f).

There was, however, an indication of a mass threshold effect. That is, the extent of the mass change at sea was related to the *relative* amount of mass the bird had lost during the previous incubation shift. An individuals average mass (after incubating for 48 hours) was subtracted from it's departure mass to provide an indication of the relative "condition" of the bird at the end of it's shift. There was a negative relationship between this measure of condition and the subsequent mass gain at sea; birds leaving in poorer condition tended to regain more mass before returning to the colony (Figure 5.15, r=-0.322, p=0.088, n=29 for males, and r=-0.365, p=0.056, n=28, for females). Condition had no effect on the duration of the subsequent foraging trip (r=0.001, p=0.296, n=34 for males and r=0.000, p=0.600, n=35 for females).

5.4 DISCUSSION

5.4.1 *Foraging patterns and associated mass changes during the breeding season*

Shy albatrosses have amongst the shortest duration foraging trips, and shortest incubation and brooding shift durations of any albatross thus far studied (Table 5.10). Short foraging trip durations are consistent with the known foraging ranges of this species (Brothers et

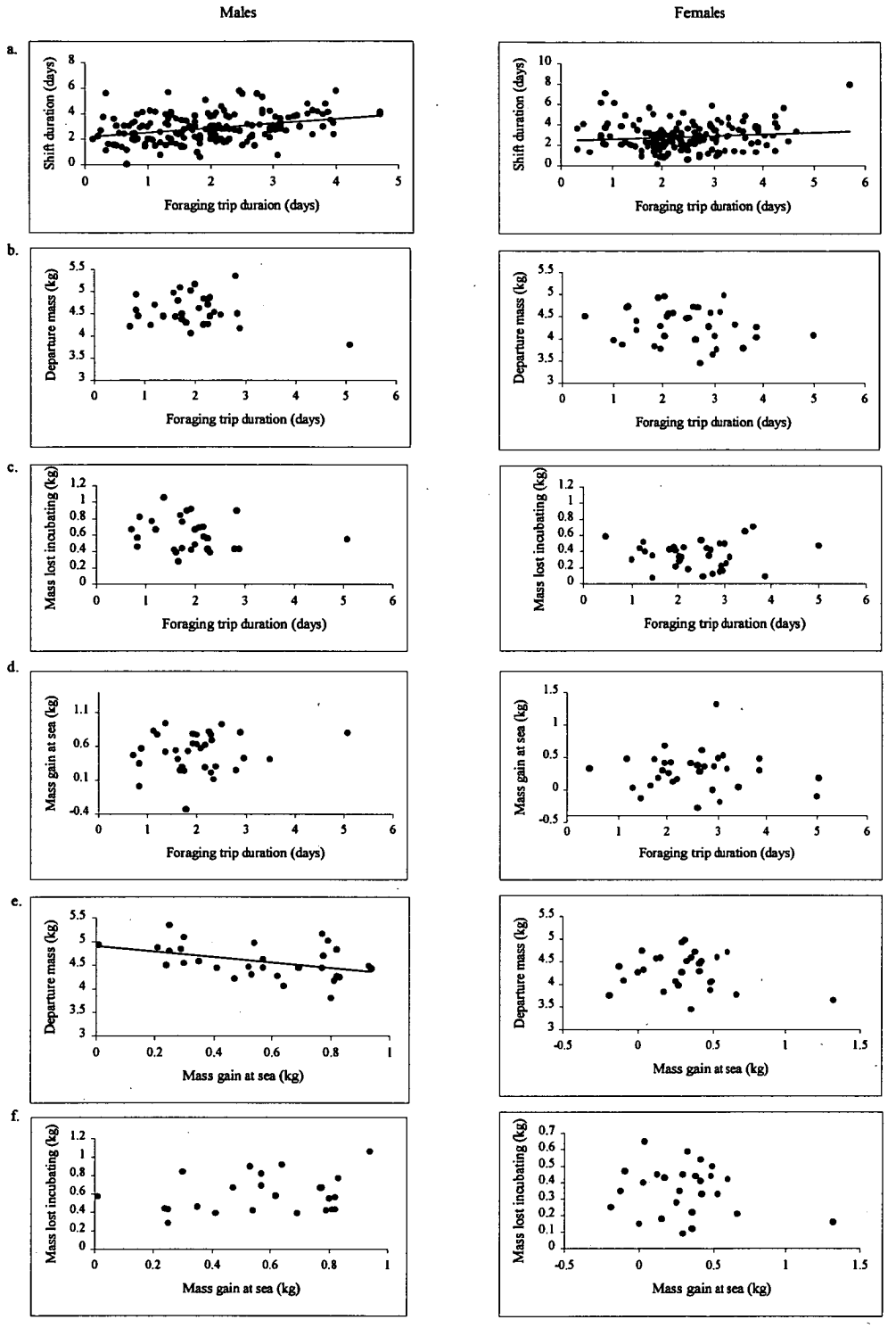


Figure 5.14: Influence of mass change on various foraging parameters of incubating male (left hand side) and female (right hand side) Shy albatrosses. Influence of (A) incubation shift duration, (B) departure mass, (C) mass lost while incubating, and (D) mass gained at sea on the duration of the subsequent foraging trip. Also, the relationship between the mass gained at sea and (E) the departure mass, and (F) the mass lost while incubating. Statistically significant relationships are indicated with a regression line.

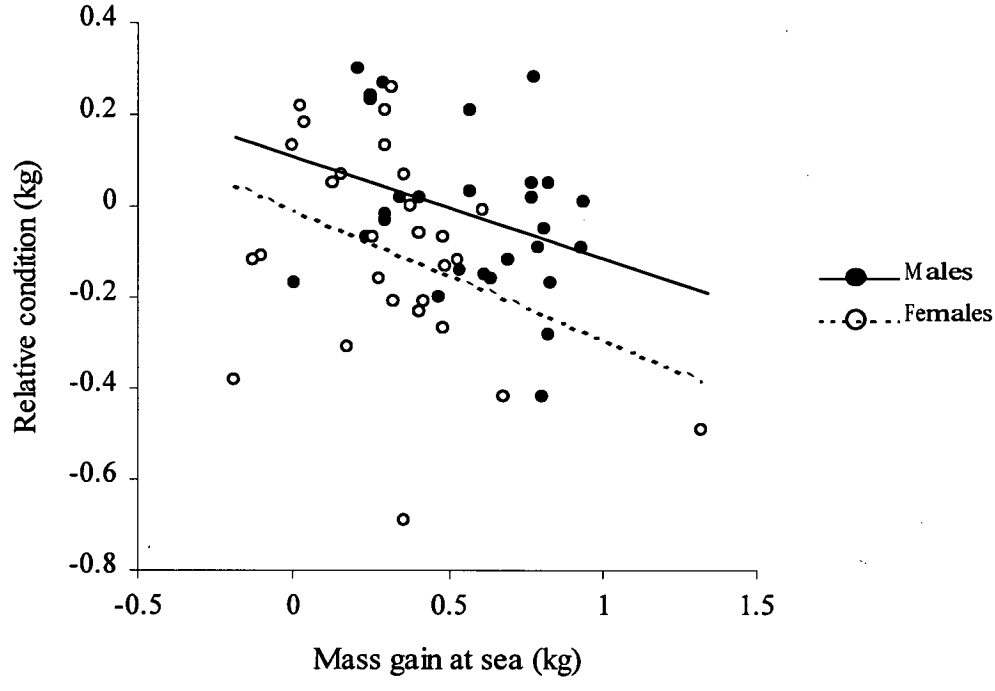


Figure 5.15: Influence of the relative condition of Shy albatrosses (departure mass - average 48 hour mass, in kg) at the end of their incubation shifts on the extent of subsequent mass gain at sea.

al. 1998, and Chapters 3 & 8), with birds from all three populations foraging in neritic waters over the southeast Australian continental shelf during the breeding season. Foraging trips are longest early in incubation and late in chick-rearing (averaging 2-3 days), when birds cover up to 1,300 km when searching for food. During chick-brood, trips are shorter and they show the least variability between individuals, breeding sites and years. Food is then generally taken at a maximum range of 100 km from the colony within 24 hours.

The life history characteristics of Shy albatrosses are largely consistent with their neritic foraging habits. Birds begin breeding at a relatively young age (5 years, N. Brothers, unpubl. data), and their breeding success is highly variable between years (although how this relates to body condition is unknown). However, in contrast to what has been found for other neritic species, Shy albatrosses appear to regulate their body mass, to some degree, during incubation by regaining mass proportionate to that lost on the nest during incubation fasts. Body mass or condition has been implicated in the breeding strategy of pelagic seabirds (regulation of foraging trip duration for female Wandering albatrosses during incubation Weimerskirch 1995, and influential in the "decision to breed" in Blue petrels, Chastel et al. 1995b), however, it has not been previously found to influence the breeding, foraging or provisioning behaviour of neritic species (Chastel et al. 1995a, Weimerskirch et al. 1997c).

Changes in the attendance and foraging patterns of Shy albatrosses throughout the breeding season are similar to patterns observed in other albatross and petrel species, with shifts at the nest shortening prior to hatching (Tickell & Pinder 1975, Weimerskirch et al. 1986, Pettit et al. 1988, Johnstone & Davis 1990, Weimerskirch et al. 1993, Lorentsen & Røv 1995). This appears to be a common feature of seabird breeding strategies, and presumably occurs so that the chick receives a feed soon after hatching (Croxall 1984).

5.4.2 *Incubation*

During incubation, Shy albatrosses spend, on average, just 2-3 days at sea and 3-4 days sitting on the nest. This is substantially shorter than the duration of incubation shifts in most other albatross species (Table 5.10), the only exceptions being Black-browed albatrosses breeding at Macquarie and Kerguelen Islands, where shifts average just three days (Gales et al. unpubl. data, Weimerskirch pers. comm.). However, the duration of incubation shifts is not species specific, and may be expected to vary between populations because of differences in the distribution and abundance of resources, distances to and

Table 5.10: Comparative breeding parameters and durations of shifts at the nest for 12 albatross species. Data are presented in days as the mean ± 1 SD with sample size (where available) in brackets. Where incubation shift numbers were indicated in literature, the first and last shifts have been excluded from means as these tend to be shorter (*).

Species	Breeding frequency	Site	Incubation period (n)	Incubation shift duration (days)	Brooding period (days)	Brood shifts duration (days)	Fledging period (days)	Source
Wandering *Diomedea exulans*	Biennial	Crozet Islands	80	14.0 ± 9.0 (11)	30	2.8 ± 0.9 (15)	-	Weimerskirch et al. 1993
		South Georgia	78.4 ± 1.17 (163)	20.5 (19)	32 (74)	2.6 (818)	278 ± 16.7 (35)	Tickell 1968; Croxall & Ricketts 1983
Royal *D. epomophora*	Biennial	Taiaroa Head	79.0 ± 0.71 (5)	-	34.6 (9)	1.9 (108)	236 ± 10.6 (17)	Richdale 1952
		Campbell Island	79.3 ± 0.99 (35)	-	-	-	-	Sorensen 1950
Amsterdam *D. amsterdamensis*	Biennial	Amsterdam Island	76 - 83 (4)	7.5 (3)	27.3 (3)	2.5 ± 1.2 (32)	261 ± 11.2 (3)	Jouventin et al. 1989
Sooty *Phoebetria fusa*	Biennial	Crozet Islands	70.7 ± 1.54 (40)	11.0 (105)*	21.3 ± 2.4 (42)	2.3 ± 1.0 (181)	164 ± 8.95 (28)	Weimerskirch et al. 1986
		Marion Island	70.1 ± 1.8 (15)	9.5 ± 4.51 (50)*	21.0 ± 2.1 (23)	1.9 ± 0.41 (51)	149 - 169 (6)	Berruti 1979
Light-mantled sooty *P. palpebrata*	Biennial	Crozet Islands	66.9 ± 1.39 (24)	11.5 (106)*	19.3 ± 3.3 (13)	2.6 ± 1.6 (72)	157 ± 10.6 (43)	Weimerskirch et al. 1986
		Marion Island	66.6 ± 1.5 (3)	14.6 ± 8.02 (15)*	21.0 ± 0.8 (4)	2.6 ± 2.37 (22)	170 - 175 (1)	Berruti 1979
		South Georgia	69.9 ± 1.3 (22)	13.2 ± 5.79 (33)	20.2 ± 2.6	2.2 ± 1.05 (46)	*c.* 141	Thomas et al. 1983
Black-browed *Thalassarche melanophrys*	Annual	Crozet Islands	-	-	22	-	125	Weimerskirch et al. 1986
		South Georgia	68.1 ± 1.2 (72)	13.0 ± 2.83 (42)	21.6 ± 2.8 (49)	2.5 (145)	116	Tickell & Pinder 1975; Prince et al. 1981; Croxall et al. 1988
							117 - 117.5	
		Macquarie Island	67 - 69 (84)	2.7 - 3.4	20.5 - 25.7 (62)	1.5 - 2.0		Gales et al. unpubl. data
		Kerguelen Island	-	3.0	-	-	-	Weimerskirch pers comm
		Campbell Island	-	-	-	-	130	Waugh & Weimerskirch 1998
Southern Buller's *T. bulleri*	Annual	The Snares	69.1 ± 1.3 (61)	10.0 ± 1.95 (150)*	15 - 30	2.4 ± 2.1 (149)	167 ± 9.7 (52)	Sagar & Warham 1998
Shy *T. cauta*	Annual	Albatross Island	73.0 ± 1.0 (62)	2.9 ± 0.68 (375)[2]	27.3 ± 3.86 (27)	1.0 ± 0.22 (653)[2]	126 ± 7.54 (11)	This study and N. Brothers unpubl. data
		Pedra Branca	-	2.9 ± 0.74 (29)[2]	-	1.0 ± 0.34 (17)[2]	-	
Yellow-nosed *T. chlororhynchos*	Annual	Amsterdam	-	12 – 15	-	-	115	Jouventin et al. 1983
Grey-headed *T. chrysostoma*	Biennial	Crozet Islands	73.2 ± 1.32 (18)	9.2 (132)*	23.1 ± 3.8 (15)	2.4 ± 1.1 (135)	*c.* 145	Weimerskirch et al. 1986
		Macquarie Island	71 - 72 (67)	4.6 - 6.4	24.1 - 25.5	2.1 - 3.1	-	Gales et al. unpubl. data
		South Georgia	72.4 ± 1.6 (103)	11.8 ± 1.10 (41)	22.6 ± 2.8 (27)	2.9 (196)	141	Tickell & Pinder 1975; Prince et al. 1981; Croxall et al. 1988
							141 - 144.4	
Waved *Phoebastria irrorata*	Annual	Hood Island	60.8 ± 1.30 (5)	20.2 ± 1.53 (73)[1]	-	2.3 (16)	167	Harris 1973
Laysan *P. immutabilis*	Annual	French Frigate Shoals	-	-	-	2.04 ± 1.04 (26)	-	Pettit et al. 1988
		Midway Atoll	64.4 ± 1.02 (95)	13.2 ± 7.67 (415)*	17.2 ± 2.47 (94)	1.9 ± 0.66 (651)*	165	Rice & Kenyon 1962
Black-footed *P. nigripes*	Annual	Midway Atoll	65.6 ± 1.18 (75)	7.7 ± 6.62 (144)*	19.1 ± 2.65 (24)	2.1 ± 0.57 (206)*	140	Rice & Kenyon 1962

[1] average of three annual means; [2] average of individual bird means

from the foraging grounds, foraging efficiencies or other aspects of the foraging ecology. For example, the 13 day incubation shifts of Black-browed albatrosses at South Georgia (Tickell & Pinder 1975) presumably result from exploitation of less predictable prey (note variation in the diet between years, Prince 1980, Reid et al. 1996), and/or prey that are located further afield. Nevertheless, the neritic foraging habits of Shy albatrosses (at least at Albatross Island) and those of Black-browed albatrosses at Kerguelen Island result in some fundamental differences in breeding and provisioning strategies, the most obvious of which are the short duration of foraging trips throughout the season.

There are no sex-specific differences in the time spent foraging at sea, or sitting on the nest during incubation or any other stage of the breeding season. Equality between the sexes at this stage is similar to observations for Black-browed and Grey-headed albatrosses, but contrasts with the situation for Wandering, and Light-mantled Sooty albatrosses *Phoebetria palpebrata,* and also Northern fulmars *Fulmarus glacialis* where the contributions of the sexes differ (Croxall & Ricketts 1983, Weimerskirch et al. 1986, Hatch 1990). Species differences likely relate to gender specific foraging locations, which are similar for Shy albatrosses (Chapter 8), but differ markedly for species such as Wandering albatrosses where the sexes segregate at sea.

On foraging trips during incubation, male Shy albatrosses gain proportionally more mass per foraging day and they gain it more rapidly than females. This is similar to findings for Wandering albatrosses breeding on the Crozet Islands in the southern Indian Ocean and on South Georgia in the south Atlantic (Croxall & Ricketts 1983, Weimerskirch 1995). The sexes of Wandering albatrosses from both localities segregate at sea, and differences in productivity of the associated water masses have been proposed to account for differences in the mass gain at sea (Prince et al. 1992, Weimerskirch et al. 1993, Weimerskirch 1995, Prince et al. 1998). However, during incubation, all foraging by Shy albatrosses occurs over the continental shelf within 300 km of the colony, with no clear separation of the areas used by males and females (Chapter 8). Differential mass gain at sea, however, does indicate some consistent sex difference in the foraging behaviour itself, or it is possibly a reflection of sex-specific metabolic rates and/or assimilation efficiencies relating to hormonal status. Given that males spend more time in the colony than females during the non-breeding period (which could also be hormonally driven), it seems possible that the differential mass gain may result from a sex difference in territoriality, or the drive to be in attendance at the site. It is plausible that the stronger male drive continues throughout incubation, and results in males regaining condition more rapidly than females.

During incubation shifts, Shy albatrosses lose a higher proportion of their body mass per day than any other albatross species studied (Table 5.11; Prince et al. 1981, Croxall 1982a, and references therein, Croxall & Ricketts 1983), and rates are similar between the sexes. While Shy albatrosses lose a comparable 12% of their initial body mass per incubation shift, the rate at which they lose the mass is remarkable, equating to almost 4% per day. These rates are up to 4-fold higher across a full incubation shift (and up to 2.5-fold higher after digestion of the stomach contents) than reports for Wandering, Grey-headed, Laysan and Black-browed albatrosses (Table 5.11; Prince et al. 1981, Croxall 1982a, Croxall & Ricketts 1983). A number of factors potentially contributing to the higher daily mass loss rates are discussed.

Table 5.11: Comparative rates of mass loss during incubation shifts for six albatross species.

Species	Breeding zone	Initial body mass (kg)	Total mass lost/shift (% initial mass)	Average daily mass loss (% initial mass)	Source
Wandering	Sub-antarctic	8.18-11.94 (19)	17 (19)	0.87-0.93 (19)	Croxall & Ricketts (1983)
Shy (full shift)	Temperate	4.99 ± 0.41 (42)	12.2 ± 6.20 (42)	4.0 ± 1.37 (42)	this study
Shy (from 48 hr)	Temperate	4.99 ± 0.41 (42)	-	2.2 ±1.38 (24)	this study
Black-browed	Sub-antarctic	3.69-3.92	17.6 ± 1.8 (42)	1.2 (42)	Prince et al. (1981)
Yellow-nosed	Temperate	-	-	1.55 (30)	Weimerskirch pers. comm.
Grey-headed	Sub-antarctic	3.62-3.75	14.6 ± 1.4 (41)	1.1 (43)	Prince et al. (1981)
Laysan	Tropical	3.00-3.30 (60)	15-18 (60)	1.1 (60)	Rice & Kenyon (1962)

Short foraging ranges indicate that Shy albatrosses catch food close to the breeding colonies, and as a result they likely return with food still in their stomachs. High initial rates of mass loss (during the first two days) likely simply result from digestion of the stomach contents and associated voiding of liquids. In support of this, the proportion of mass lost per day was halved and constant after 48 hours. Pelagic species, in contrast, are likely to return with less food in their stomachs; prey being caught far from the breeding colony and digested prior to the bird's return. For example, when incubating, both

Wandering albatrosses and King penguins *Aptenodytes patagonicus* return to the breeding colonies with empty stomachs (Weimerskirch pers. comm., Cherel et al. 1993).

There is a also a characteristic metabolic depression for species which fast for long periods (Cherel et al. 1988), and it may be that this depression occurs less rapidly, if at all, in short-term fasters such as Shy albatrosses. Support for a delay in metabolic depression is provided by examining the proportion of mass lost by the male that incubated for 32 days. While this bird lost 1.35% of his initial body mass per day across the entire shift, when the first two days were excluded, just 1.01% of initial body mass was lost each day. This latter figure is similar to the rates reported for the long-term fasting species (Table 5.11).

While proximity to the feeding grounds and a potential delay in metabolic depression can account for the high mass loss rates early in incubation shifts, the fact that mass loss continues (at an average of 2.2% per day) following digestion of the stomach contents indicates further endogenous differences between Shy and other albatross species. The most plausible explanation is an elevated rate of water loss in Shy albatrosses. This could be manifested through differences in the nature of the tissues catabolized, along with increased evaporative water loss. Pelagic species rapidly convert food into fat stores (Weimerskirch pers. comm.), and they mainly use these stores to fuel their lengthy fasts (Cherel et al. 1988 & 1994, Groscolas 1988). In fact, up to 93% and 96% of the energy required by King and Emperor penguins, respectively, during their fasts results from oxidation of lipids, and the remainder from oxidation of protein (Groscolas 1988, Cherel et al. 1994). Species that forage in the neritic environment, and fast for shorter periods of time, are not as efficient at protein sparing and also not as reliant on fat storage or utilization (see Cherel et al. 1993). For example during 12 days of fasting, Gentoo penguins, which normally fast for 2.4 days during incubation (Bost & Jouventin 1991), derived 15% of total energy expenditure from protein (Cherel et al. 1993), two to four times that for Emperor and King penguins, respectively. Also, as 5.5 g of water are lost for each gram of protein utilized (Cherel et al. 1993), and as protein has a lower energetic value than lipid, Gentoo penguins lost more overall and more specific body mass than King penguins (Cherel et al. 1993). The effectiveness of protein sparing also appears to be related to initial adipodisity, which is typically lower in Gentoo than in King penguins (Cherel et al. 1993).

If similar to the composition of the mass lost by Gentoo penguins, then the relatively high rates of mass loss by Shy albatrosses may be at least partially explained by the nature of the fuels used. Indeed, assuming similar compositions resulted in metabolic estimates

that lay in between BMR and EMR during incubation. The 112 g/day lost by Shy albatrosses, would equate to daily losses of 33.7 g of fat, 12.1 g of protein and 66.2 ml of water. High water influx rates (68 ± 47 ml/kg/day, Green et al. unpubl. data) have been noted for fasting, incubating Shy albatrosses, indicating that substantial water is produced via oxidation of the body stores.

Differences in the fasting mass loss rates of Shy albatrosses between incubation (spring/summer) and winter, indicate that evaporative water loss also likely played a role. Located just south of 40°, the climate at Albatross Island is temperate (daily maximum temperatures in the summer months average 19-21° C, and 13-15° C in winter), and differs substantially from conditions encountered by birds breeding in the sub-Antarctic where average temperatures range from 1-5° C (Clark & Dingwall 1985). While daily mass loss rates from 48 hours were not statistically different between spring/summer and winter, rates in winter were lower (1.7 vs 2.2% per day). Also, the estimates of metabolic rate made from rates of mass loss during winter, when evaporative water loss would be expected to be lower, were closer to theoretical predictions.

Supporting increased rates of evaporative water loss, is data from the Indian Yellow-nosed albatross *Diomedea chlororhynchos* breeding at Amsterdam Island (37.5 °S), where temperatures and weather patterns are comparable to those at Albatross Island (Weimerskirch pers. comm.). Yellow-nosed albatrosses have long shifts on the nest during incubation (average 12-15 days, range 5-20 days, n=30, Weimerskirch pers. comm.), but their rates of mass loss were somewhat higher than expected, averaging 1.55% per day (range 0.8-2.6%, Weimerskirch pers. comm.). It seems plausible then that increased ambient temperatures and attendant increases in evaporative water loss may result in higher proportional mass loss rates for albatrosses breeding in temperate as opposed to sub-Antarctic latitudes. Metabolic costs associated with behavioural responses to overheating (i.e., panting, which is commonly observed in Shy albatrosses) may also contribute to increased mass loss rates. It is worth noting that the mass loss rates for Laysan albatrosses, which breed in the tropics, are in line with observations from other long-term fasting species (Croxall 1982a). Water turnover rates, however, suggest that these birds encounter a water deficit of 9 ml/kg/day (Petit et al. 1988). However, if they are typical of long-term fasters, and utilize mainly fat and spare protein, this would certain stem their rates of water loss. Irregardless of the proximate cause, the high mass/water loss rates of Shy albatrosses warrant further study.

In pelagic seabirds, short foraging trips during incubation are said to be inefficient because of the proportionately greater amount of time required to travel to the foraging grounds (Hatch 1990). The foraging strategy of Shy albatrosses employs short duration foraging trips to exploit locally abundant and accessible resources in the neritic environment. A number of factors indicate that this strategy permits a substantial degree of flexibility in the time-energy budget, or said another way, it appears that Shy albatrosses have a wider "error margin" built into their breeding strategy. The high degree of inter-pair variability and the lack of inter-annual variation in attendance patterns, along with the high proportion of arrivals during incubation which do not result in nest changeovers, indicate that Shy albatrosses are operating in a somewhat flexible system. It seems that a variety of strategies can carry individuals through incubation, with mean foraging trip durations for successful pairs ranging from less than one day to more than four days. While undoubtedly extreme, the extent of this error margin is demonstrated by the 32-day incubation shift of the R35 male during November 1997. Such flexibility could possibly account for the largely negative results for relationships between foraging parameters and body mass/condition changes during this stage.

5.4.3 *Chick-brooding*

Shy albatrosses brood their chicks for an average of 27 days in a series of 24 hour shifts prior to first leaving them alone at the nest. The brooding period is slightly longer in absolute terms, and also slightly longer as a proportion of the total fledging period (approximately 20%) than the 12-18% reported for the other small albatross species (Table 5.10), perhaps further demonstrating their flexibility. However, the lack of individual, gender, inter-annual, and site specific variation in foraging trip and shift durations at the nest indicates that during this stage birds have a limited amount of time to locate food for themselves and their chick. The general decline in body mass indicates that chick-brood may be an energetically demanding period for Shy albatrosses, however, as we have no data on body mass later in the season, the decrease is difficult to interpret. Chick-brood is known to be demanding for a number of other albatross species, as similar declines in body mass have been reported for Black-browed, Grey-headed and Wandering albatrosses (Prince et al. 1981, Croxall 1990, Salamolard & Weimerskirch unpubl. data cited in Salamolard & Weimerskirch 1993). The body mass decline continues throughout the rearing period for both Black-browed and Grey-headed albatrosses (Croxall 1990), while, using a different foraging strategy, Wandering albatrosses regain condition while raising their chicks (Salamolard & Weimerskirch unpubl. data, cited in Salamolard & Weimerskirch 1993, Weimerskirch et al. 1994 & 1997b).

5.4.4 *Chick-rearing*

The expenditure of breeding effort in Southern pelagic seabirds is thought to be under the strict control of adult body condition (Chaurand & Weimerskirch 1994a, Chaurand & Weimerskirch 1994b, Weimerskirch et al. 1994, Chastel et al. 1995a, Chastel et al. 1995b, Weimerskirch et al. 1997b). In the Blue petrel, body condition early in the season influences the decision to breed, correlates with inter-annual variation in breeding success (Chastel et al. 1995a, Chastel et al. 1995b), and from the timing of egg desertions, indicates a mass threshold for nest abandonment (Chaurand & Weimerskirch 1994a). When rearing chicks, pelagic species either alternate or mix short and long foraging trips, and in the species studied, behavioural decisions appear to be based solely upon the status of adult body reserves (Chaurand & Weimerskirch 1994b, Weimerskirch et al. 1994, Weimerskirch et al. 1997b). In general, adult body mass increases following long foraging trips into pelagic waters, but decreases after short neritic trips. The evolution of this two-fold strategy appears to be a compromise between balancing the adults energy budget and meeting the chicks provisioning requirements throughout the rearing period (Weimerskirch et al. 1994, Weimerskirch et al. 1997b).

In contrast, Shy albatrosses perform only short foraging trips, returning to feed their chick, on average, every two days throughout the rearing period. In terms of the brevity of foraging trips, Shy albatrosses are similar to Black-browed albatrosses on both Kerguelen Island and South Georgia, where only short (two day) trips are also performed during this stage (Weimerskirch et al. 1997c, Prince et al. 1998, Weimerskirch 1998b). While the body mass of individual Black-browed albatrosses varied greatly from one trip to the next, the extent of the mass change did not relate to either the duration of the subsequent foraging trip nor to the size of the meal next delivered to the chick (Weimerskirch et al. 1997c). Body mass was therefore reported not to influence the provisioning strategy of this species at Kerguelen Island. This may also be the case for Shy albatrosses, however, as no body mass data were collected for adults post-brood, this possibility could not be explored.

Chicks fledge after spending 127 ± 7.4 days (n=10) in the nest. High food delivery rates combined with a diet composed largely of fish (Chapter 6), results in rapid chick growth (Chapter 7), and this plausibly decreases the duration of the chick-rearing period (Table 5.10). Yellow-nosed albatrosses fledge their chicks in just 115 days (Jouventin et al. 1983), and they have the highest growth rates recorded for any albatross species (Weimerskirch et al. 1986). Shy and Black-browed albatrosses have similarly short fledging periods (127 vs 116-125 days), approximately 15-25 days shorter than Grey-

headed and Light-mantled sooty albatrosses which enjoy the next shortest fledging periods.

Single parent feeding seems an unfeasible option for pelagic species, as adults never allow their body condition to critically deteriorate (Drent & Daan 1980). If one member of a pelagic pair deserts a breeding attempt during the rearing period, the chick will almost certainly die. We have found in this and concurrent provisioning studies (Chapter 7), that depending on the individual involved, single Shy albatrosses are capable of fledging a chick. Early nest desertions accompanied by successful breeding outcomes were observed four times in this study, with the single parents in question feeding alone for periods ranging between six and 12 weeks. In at least one of these instances (R45 female which fed alone for 12 weeks in 1996/97), the number of deliveries to the chick was significantly increased relative to the performance of dual-parent chicks, as well as relative to this birds own performance in years when she feed along with her partner. This indicates not only that chicks can convey their nutritional status to their parents, but also that some individuals have the capacity to act upon this information and appropriately increase their provisioning rate. The fact that the provisioning rate of some single parents was indistinguishable from birds feeding along with their mates, coupled with the fact that not all single parents were successful, indicates that individual quality is an important factor determining the regulation capability of a species. The influence of individual quality is increasingly being recognized as predictive of breeding outcomes (Becker 1998, Cobley et al. 1998).

Despite the superior performance of some individuals, the pattern of nest desertion during mid to late chick rearing indicates that this is also an energetically stressful time for this species. Five of the observed nest failures at Albatross Island occurred during late chick rearing, and for three of these pairs, the death of the chick was precipitated by variable periods of single parent attendance. In this study chicks had little greater than 50% (four of seven) chance of survival if one of its parents deserted post-brood. For three of the five late-failing nests, and in three of the four successful single parent nests, parents deserted within a couple of weeks of each other, between early and mid-February when their chicks were 10-12 weeks old. The consistency in the timing of the nest desertions both between individuals and years, are indicative of high energy demands at the nest.

5.4.5 *Comparison between the breeding sites*

Attendance patterns of Shy albatrosses breeding at Albatross Island and Pedra Branca were similar. At both sites birds incubated and brooded chicks for similar durations, and

fed chicks at similar intervals throughout the rearing period. Information on the foraging location of Pedra Branca birds indicates that they too feed over the continental shelf, off southern Tasmania (Chapter 8). The distances they travel during incubation and chick-brood are comparable to Albatross Island (Brothers et al. 1998, and Chapters 3 & 8).

5.4.6 *Failed vs successful breeders*

The only difference in foraging characteristics between successful and failed breeding Shy albatrosses occurred during chick-brood, when unsuccessful pairs spent longer on the nest. Seven of the 18 breeding failures at Albatross occurred during early incubation, and despite this, foraging trip and shift durations were indistinguishable between these and successful pairs. However, relative to successful breeders, failed breeders made a higher proportion of visits to the colony without nest changeovers, perhaps indicating less co-ordination between unsuccessful pairs. This was similar to the situation with Adélie penguins *Pygoscelis adeliae* where co-ordination of effort within pairs, especially during incubation, was strongly implicated in both successful breeding outcomes and mate retention (Davis 1988). As nest failures during early incubation occurred between field trips, it is not known whether they resulted from broken or infertile eggs, or were simply the result of nest abandonments. Nest failures did not often result from extended incubation shifts, and this finding was similar to that of Weimerskirch (1995) for Wandering albatrosses. Extended incubation shifts appeared to result in breeding failure only once in this study, after the 32-day shift by the R35 male in 1997/98. Considering the fasting capacity of this species relative to the brevity of normal incubation shift durations, this is perhaps not surprising. Hatch (1990) also found the mean duration of incubation shifts to be similar between failed and successfully breeding Fulmars. He, however, suggested that it was occasionally unsuccessful foraging trips, rather that the accumulation of small differences throughout incubation, which were responsible for some of the failures he observed.

Late-failing and successful breeders also differed in the relative amount of time spent on the nest early in the breeding season, with failing pairs spending longer periods incubating and brooding the chick. The sex difference scores of failing pairs were also less than those of successful pairs, indicating that failing females contributed more to the breeding attempt. Croxall & Ricketts (1983) also found an increased probability of breeding failure when female Wandering albatrosses contributed more than average to incubation.

5.4.7 *Inter-annual variation*

Pairs which fledged their chick had similar attendance cycles and foraging trip durations in all years, perhaps indicating that food was comparably available between years. While there were inter-annual differences in breeding success, and such differences can generally be linked with resource availability, the confounding influence of an avian pox virus on Albatross Island makes it inappropriate to use breeding productivity as an index of food availability at this site. The magnitude of the virus and its effects on breeding productivity vary greatly between years, but breeding success can be lowered to just 10% in some colonies in some years (N. Brothers, unpubl. data).

From concurrent provisioning work (Chapter 7), we know that there is often an inequality in the provisioning performance within breeding pairs, and this is unrelated to sex. The direction of the inequality tends to be consistent, with good and poor providers behaving similarly from year to year. An analogous finding has been reported for Adélie penguins, with the foraging trip durations of individuals during incubation tending to be similar from one year to the next (Davis 1988). In Shy albatrosses the degree of inter-pair variability in foraging parameters is high, and this along with the tendency for individuals to behave relatively consistently from year to year, may make longitudinal studies fruitful for addressing inter-annual variation in this species

5.4.8 *Colony attendance during the non-breeding period*

While most other albatrosses traverse the high seas during their non-breeding period (Nicholls et al. 1992 & 1995, Prince et al. 1998), Shy albatrosses are unique in spending only two months at sea after fledging their chicks. After spending a longer period at sea, the previous seasons failed breeders return to the colony earlier than birds that fledged their chick. Birds return between April and June and they subsequently spend much of the austral winter attending the site. Given what we know of the distribution of adults immediately after fledging, combined with their over-winter attendance patterns, it appears that adults remain in southeast Australian waters throughout the non-breeding period (Brothers et al. 1997 & 1998, and Chapters 3 & 8). Prey resources in the wider continental shelf region must therefore be sufficient to support the energy requirements of these populations year round.

5.5 CONCLUSIONS

Seabird life history characteristics are intimately linked with features of the marine environment the birds exploit. Highly seasonal or inter-annual 'boom and bust' cycles characteristic of Antarctic and sub-Antarctic systems would likely have little influence on

species breeding within the temperate zone. The distribution and abundance of prey within Shy albatross foraging zones makes profitable their strategy of repeatedly searching patches of continental shelf waters close to their colonies. Birds generally locate food for themselves and for their single chick in less than three days. There appears to be substantial flexibility or, alternatively, large safety margins in the breeding strategy at least during the incubation period. Birds generally fast for no longer than four days, while their fasting capacity exceeds 30 days. However, from elevated patterns of mass loss, there is some indication that ambient temperatures, which range from 13-15 °C in winter to 19-21 ° C in summer, may constrain the duration of shifts during this stage, with short shifts perhaps required for maintenance of water balance. Working longitudinally at the level of the individual it was apparent not only that there were substantial individual differences but also that individuals behaved relatively consistently from one year to the next. Differences in individual quality were substantial, especially during the chick-rearing period, when quality was highly correlated with breeding success. In order to understand the evolution of contrasting seabird life history strategies, especially in closely related species, it is essential to work at the level of the individual bird, both with respect to breeding outcomes on land and foraging behaviour at sea.

Appendix 5A: The duration of foraging trips for successful paris of Shy albatrosses (those which fledged their chick) during the 1995-96, 1996-97 and 1997-98 breeding seasons. Data are presented for each member of the pair as the mean ± 1 SD, with the sample size given in parentheses.

		Males					Females				
Year	Nest	Early Inc	Late Inc	Brooding	Early Chick	Late Chick	Early Inc	Late Inc	Brooding	Early Chick	Late Chick
	R35	2.0 ± 0.59 (7)	2.0 ± 0.38 (2)	1.0 ± 0.33 (16)	1.1 ± 0.58 (26)	1.7 ± 1.34 (28)	1.1 ± 0.54 (16)	1.8 ± 0.99 (3)	0.9 ± 0.23 (16)	1.3 ± 0.88 (22)	2.2 ± 1.68 (20)
	I3	1.0 ± 0.22 (9)	1.1 ± 0.44 (4)	1.0 ± 0.39 (21)	1.0 ± 0.69 (27)	1.9 ± 1.31 (33)	3.4 ± 0.88 (3)	2.3 ± 0.65 (2)	1.0 ± 0.23 (18)	1.0 ± 1.09 (26)	2.7 ± 2.75 (18)
	R1	0.8 ± 0.53 (19)	1.5 ± 0.45 (4)	0.6 ± 0.25 (18)	0.9 ± 0.48 (26)	1.8 ± 1.32 (25)	0.9 ± 0.48 (20)	1.4 ± 0.59 (3)	0.8 ± 0.42 (19)	1.3 ± 1.05 (20)	2.0 ± 1.35 (30)
1995-96	R45	1.6 ± 0.95 (9)	1.1 ± 1.03 (2)	0.9 ± 0.62 (20)	1.3 ± 1.44 (21)	2.0 ± 1.69 (32)	2.4 ± 1.00 (6)	2.1 ± 0.60 (3)	0.7 ± 0.31 (20)	0.8 ± 0.47 (35)	1.8 ± 1.35 (40)
	Z3[a]	2.0 ± 0.87 (10)	1.6 ± 0.36 (4)	1.0 ± 0.33 (13)	1.0 ± 0.50 (23)	2.2 ± 1.50 (31)	2.1 ± 0.73 (10)	1.1 ± 0.44 (4)	1.4 ± 1.37 (12)	1.5 ± 1.28 (14)	2.2 ± 2.03 (9)
	Z5[b]	-	-	0.7 ± 0.28 (8)	1.5 ± 1.31 (8)	-	-	-	1.0 ± 0.35 (10)	1.1 ± 0.76 (22)	1.3 ± 0.86 (48)
	Z6[c]	-	-	0.8 ± 0.52 (7)	1.0 ± 0.62 (24)	1.6 ± 0.94 (24)	-	-	1.3 ± 1.53 (8)	1.0 ± 0.56 (26)	1.9 ± 1.11 (36)
	Z7[d]	-	-	0.8 ± 0.33 (6)	1.2 ± 0.53 (17)	2.2 ± 1.66 (28)	-	-	0.8 ± 0.17 (12)	1.0 ± 0.52 (30)	1.6 ± 1.07 (43)
overall		**1.5 ± 0.56**	**1.5 ± 0.38**	**0.9 ± 0.15**	**1.1 ± 0.20**	**1.9 ± 0.19**	**2.0 ± 1.02**	**1.7 ± 0.49**	**1.0 ± 0.25**	**1.1 ± 0.23**	**2.0 ± 0.42**
	I3[e]	1.2 ± 0.80 (22)	1.1 ± 0.64 (4)	0.8 ± 0.50 (15)	0.9 ± 0.67 (26)	1.5 ± 0.97 (33)	3.6 ± 0.81 (8)	1.8 ± 1.09 (3)	0.9 ± 0.32 (13)	1.8 ± 1.26 (15)	3.3 ± 2.24 (5)
	R45[f]	1.7 ± 0.72 (14)	1.9 ± 0.12 (2)	1.0 ± 0.62 (17)	1.0 ± 0.61 (5)	-	2.0 ± 0.85 (15)	1.7 ± 1.03 (3)	0.8 ± 0.32 (15)	0.8 ± 0.54 (35)	1.0 ± 0.58 (64)
	Z8[g]	2.6 ± 0.77 (9)	0.6 ± 0.41 (7)	1.0 ± 0.15 (13)	1.9 ± 1.72 (9)	-	3.8 ± 1.51 (5)	0.8 ± 0.34 (4)	0.8 ± 0.27 (12)	1.1 ± 0.63 (23)	2.0 ± 1.56 (33)
	Z9[h]	2.6 ± 1.31 (7)	1.7 ± 1.44 (4)	0.8 ± 0.22 (17)	0.7 ± 0.51 (9)	-	3.3 ± 0.68 (7)	1.0 ± 0.38 (3)	0.8 ± 0.41 (18)	-	-
1996-97	Z7	1.6 ± 0.62 (15)	1.1 ± 0.25 (4)	0.7 ± 0.15 (12)	1.0 ± 0.44 (18)	2.6 ± 1.01 (19)	2.4 ± 0.82 (17)	1.6 ± 0.55 (3)	1.1 ± 0.42 (16)	1.0 ± 0.37 (23)	1.5 ± 0.98 (33)
	Z10	2.6 ± 0.98 (8)	2.1 ± 0.50 (3)	0.8 ± 0.40 (18)	0.8 ± 0.44 (26)	2.4 ± 2.60 (21)	2.7 ± 1.28 (9)	1.4 ± 0.53 (4)	0.7 ± 0.15 (15)	0.9 ± 0.52 (20)	2.0 ± 1.52 (17)
	Z12	2.6 ± 0.92 (9)	1.1 ± 0.20 (3)	0.8 ± 0.35 (15)	1.3 ± 0.82 (16)	3.4 ± 2.59 (16)	2.6 ± 0.88 (8)	0.9 ± 0.64 (6)	0.8 ± 0.46 (14)	0.9 ± 0.77 (27)	3.3 ± 3.8 (11)
	Z13	1.5 ± 0.82 (12)	1.7 ± 0.21 (2)	0.7 ± 0.27 (18)	1.0 ± 0.82 (22)	3.1 ± 2.60 (17)	1.7 ± 1.06 (8)	2.0 ± 0.94 (2)	0.9 ± 0.53 (16)	1.0 ± 0.69 (25)	1.6 ± 1.10 (36)
	Z14	2.4 ± 0.78 (11)	1.8 ± 0.65 (3)	1.1 ± 0.40 (15)	1.4 ± 0.81 (13)	2.3 ± 1.76 (28)	1.7 ± 0.68 (10)	1.2 ± 0.21 (3)	0.9 ± 0.23 (18)	1.1 ± 0.50 (18)	5.3 ± 3.57 (10)
	Z16[i]	1.3 ± 0.38 (12)	1.0 ± 0.41 (3)	0.8 ± 0.27 (15)	1.0 ± 0.46 (18)	1.8 ± 1.69 (19)	2.5 ± 1.08 (10)	2.3 ± 1.18 (3)	1.0 ± 0.67 (16)	1.0 ± 0.65 (16)	3.2 (1)
overall		**2.0 ± 0.60**	**1.4 ± 0.49**	**0.9 ± 0.14**	**1.1 ± 0.35**	**2.4 ± 0.67**	**2.5 ± 0.93**	**1.5 ± 0.50**	**0.9 ± 0.12**	**1.1 ± 0.29**	**2.0 ± 1.07**
	R45	2.4 ± 0.79 (11)	2.4 ± 0.29 (3)	1.0 ± 0.47 (12)	1.3 ± 0.81 (20)	2.3 ± 1.34 (33)	2.4 ± 0.93 (11)	1.6 ± 0.00 (1)	0.9 ± 0.40 (12)	1.0 ± 0.70 (25)	1.9 ± 1.89 (37)
	Z7	2.8 ± 0.86 (11)	2.2 ± 0.80 (3)	1.0 ± 0.47 (5)	1.6 ± 0.94 (15)	2.6 ± 2.32 (23)	2.4 ± 0.89 (12)	1.1 ± 0.09 (2)	0.9 ± 0.15 (8)	1.4 ± 0.70 (23)	1.6 ± 1.09 (50)
1997/98	V5	1.0 ± 0.50 (13)	1.1 ± 0.49 (4)	0.8 ± 0.24 (16)	1.2 ± 0.68 (21)	1.8 ± 1.23 (25)	2.1 ± 0.56 (14)	1.8 ± 0.33 (3)	0.9 ± 0.40 (17)	1.1 ± 0.65 (25)	2.4 ± 1.94 (18)
	V8	1.7 ± 0.55 (7)	1.7 ± 0.70 (3)	1.3 ± 0.54 (14)	1.3 ± 0.95 (21)	2.4 ± 1.60 (29)	1.7 ± 0.63 (12)	1.9 ± 0.32 (2)	1.0 ± 0.39 (14)	1.1 ± 0.51 (25)	1.9 ± 1.82 (32)
	nextZ8[j]	2.3 ± 0.92 (11)	1.3 ± 0.39 (3)	1.1 ± 0.41 (12)	1.2 ± 0.71 (22)	1.7 ± 1.77 (30)	3.2 ± 0.98 (8)	2.5 ± 1.09 (2)	1.0 ± 0.52 (12)	-	-
	Z13 new[k]	2.6 ± 0.89 (9)	2.3 ± 0.41 (2)	1.0 ± 0.36 (9)	-	-	1.9 ± 0.50 (11)	1.4 ± 0.54 (3)	0.9 ± 0.20 (11)	1.1 ± 0.66 (23)	1.7 ± 1.05 (50)
overall		**2.1 ± 0.67**	**1.8 ± 0.55**	**1.0 ± 0.16**	**1.3 ± 0.16**	**2.2 ± 0.39**	**2.3 ± 0.53**	**1.7 ± 0.48**	**0.9 ± 0.05**	**1.1 ± 0.15**	**1.9 ± 0.31**

[a] female deserted late chick-rearing; [b,c,d] transmitters attached during chick brooding; [b] male's transmitter failed early chick-rearing ; [c] male deserted late chick-rearing; [e] female deserted late chick-rearing; [f] male deserted early chick-rearing; [g] male's transmitter failed early chick-rearing; [h] male's transmitter failed during early chick -rearing, female's transmitter failed during chick-brooding; [i] male's and female's transmitters failed late chick-rearing.; [j] female's transmitter failed during chick-brooding; [k] only male carried transmitter.

Appendix 5B: Shift durations at the nest for successful pairs of Shy albatrosses (those which fledged their chick) during the 1995-96, 1996-97 and 1997-98 breeding seasons. Data are presented for each member of the pair as the mean ± 1 SD, with the sample size given in parentheses.

		Males			Females		
Year	Nest	Early Inc	Late Inc	Brooding	Early Inc	Late Inc	Brooding
	R35	3.0 ± 1.39 (8)	2.3 ± 0.59 (2)	0.8 ± 0.28 (16)	2.3 ± 0.47 (7)	2.1 ± 0.32 (2)	1.0 ± 0.34 (16)
	I3	3.2 ± 0.92 (5)	2.0 ± 0.00 (1)	0.9 ± 0.34 (19)	3.8 ± 0.72 (4)	4.1 ± 1.21 (2)	1.1 ± 0.23 (18)
	R1	2.0 ± 0.63 (12)	1.4 ± 0.55 (3)	0.9 ± 0.36 (17)	2.0 ± 0.77 (12)	2.0 ± 0.56 (3)	0.7 ± 0.29 (17)
1995-96	R45	2.8 ± 1.16 (7)	2.0 ± 0.24 (2)	0.9 ± 0.33 (19)	3.0 ± 1.44 (7)	2.0 ± 1.17 (3)	0.9 ± 0.49 (18)
	Z3[a]	2.3 ± 0.68 (10)	1.1 ± 0.46 (4)	1.2 ± 1.27 (12)	2.3 ± 0.93 (11)	1.7 ± 0.54 (4)	1.0 ± 0.22 (12)
	Z5[b]	-	-	1.3 ± 0.49 (9)	-	-	1.0 ± 0.53 (10)
	Z6[c]	-	-	0.6 ± 0.29 (8)	-	-	0.9 ± 0.61 (9)
	Z7[d]	-	-	1.6 ± 0.53 (7)	-	-	0.8 ± 0.61 (9)
overall		**2.7 ± 0.50**	**1.8 ± 0.49**	**1.0 ± 0.32**	**2.7 ± 0.73**	**2.4 ± 0.97**	**0.9 ± 0.13**
	I3[e]	3.9 ± 1.10 (8)	1.6 ± 0.68 (2)	1.1 ± 0.31 (15)	4.4 ± 0.96 (8)	2.2 ± 0.28 (3)	1.1 ± 0.60 (13)
	R45[f]	3.0 ± 0.89 (12)	1.4 ± 0.88 (2)	1.0 ± 0.40 (18)	2.4 ± 0.62 (12)	2.4 ± 0.46 (3)	1.0 ± 0.38 (16)
	Z8[g]	3.8 ± 1.73 (6)	1.5 ± 0.65 (2)	0.8 ± 0.33 (13)	4.4 ± 2.05 (6)	2.4 ± 1.24 (3)	1.0 ± 0.18 (12)
	Z9[h]	3.5 ± 0.60 (7)	1.3 ± 0.63 (4)	0.8 ± 0.27 (17)	3.1 ± 1.16 (7)	1.8 ± 1.76 (3)	0.8 ± 0.22 (18)
1996-97	Z7	2.8 ± 0.71 (15)	1.6 ± 0.50 (3)	1.3 ± 0.45 (13)	1.7 ± 0.66 (15)	1.5 ± 0.95 (3)	0.7 ± 0.24 (14)
	Z10	3.6 ± 0.43 (7)	1.9 ± 0.06 (3)	0.7 ± 0.17 (16)	2.9 ± 0.85 (7)	1.6 ± 0.60 (3)	0.9 ± 0.44 (15)
	Z12	2.8 ± 0.83 (9)	1.5 ± 0.60 (3)	0.8 ± 0.44 (15)	2.9 ± 0.88 (9)	1.5 ± 0.65 (4)	0.8 ± 0.21 (14)
	Z13	2.6 ± 1.56 (7)	2.8 ± 0.53 (2)	1.0 ± 0.39 (15)	3.7 ± 2.03 (6)	2.6 ± 0.56 (2)	0.9 ± 0.35 (15)
	Z14	2.6 ± 0.75 (9)	1.5 ± 0.15 (2)	1.1 ± 0.32 (15)	3.4 ± 1.44 (9)	2.9 ± 1.80 (3)	1.1 ± 0.38 (15)
	Z16[i]	2.7 ± 1.02 (11)	2.3 ± 1.1 (3)	1.1 ± 0.42 (14)	1.6 ± 1.16 (11)	1.0 ± 0.41 (3)	1.0 ± 0.38 (16)
overall		**3.1 ± 0.51**	**1.7 ± 0.47**	**1.0 ± 0.19**	**3.1 ± 0.98**	**2.0 ± 0.60**	**0.9 ± 0.13**
	R45	2.8 ± 0.61 (10)	1.7 ± 0.29 (2)	0.9 ± 0.34 (11)	3.2 ± 0.92 (10)	5.0 ± 0.00 (1)	1.2 ± 0.48 (12)
	Z7	3.1 ± 0.93 (11)	2.3 ± 0.81 (3)	1.7 ± 0.59 (6)	2.8 ± 1.08 (12)	1.3 ± 0.29 (2)	1.0 ± 0.40 (6)
1997/98	V5	3.3 ± 0.95 (10)	1.7 ± 0.13 (3)	1.0 ± 0.29 (16)	1.8 ± 0.75 (9)	1.6 ± 0.82 (3)	0.9 ± 0.26 (16)
	V8	3.8 ± 1.51 (7)	3.0 ± 1.06 (2)	1.1 ± 0.53 (14)	2.4 ± 0.33 (7)	3.4 ± 0.00 (1)	1.4 ± 0.63 (13)
	next Z8	3.3 ± 1.53 (8)	2.2 ± 0.88 (3)	1.0 ± 0.48 (12)	3.5 ± 1.20 (8)	1.1 ± 0.15 (2)	1.1 ± 0.42 (12)
	Z13new	2.1 ± 0.65 (10)	1.6 ± 0.59 (2)	1.1 ± 0.53 (9)	2.5 ± 0.93 (9)	2.1 ± 0.46 (3)	0.8 ± 0.39 (11)
overall		**3.1 ± 0.58**	**1.9 ± 0.80**	**1.1 ± 0.29**	**2.7 ± 0.61**	**2.4 ± 1.51**	**1.1 ± 0.22**

[a] female deserted late chick-rearing; [b,c,d] transmitters attached during chick brooding; [b] male's transmitter failed early chick-rearing ; [c] male deserted late chick-rearing; [e] female deserted late chick-rearing; [f] male deserted early chick-rearing; [g] male's transmitter failed early chick-rearing; [h] male's transmitter failed during early chick -rearing, female's transmitter failed during chick-brooding; [i] male's and female's transmitters failed late chick-rearing.

Appendix 5C: The duration of foraging trips for pairs of Shy albatrosses which became failed breeders during the 1995-96, 1996-97 or 1997-98 breeding seasons. Data are presented for each member of the pair, until the stage in which they failed, as the mean ± 1 SD, with the sample size given in parentheses. As failures occurred throughout the season, stage means were not calculated.

		Males					Females				
Year	Nest	Early Inc	Late Inc	Brooding	Early Chick	Late Chick	Early Inc	Late Inc	Brooding	Early Chick	Late Chick
	A1	0.8 ± 0.42 (8)	-	-	-	-	0.7 ± 0.38 (11)	-	-	-	-
	R21[a]	0.7 ± 0.43 (18)	1.0 ± 0.54 (6)	0.6 ± 0.24 (18)	0.7 ± 0.45 (31)	1.2 ± 0.78 (17)	0.9 ± 0.42 (10)	0.8 ± 0.12 (3)	0.7 ± 0.38 (15)	0.8 ± 0.60 (28)	3.8 ± 3.72 (8)
1995-96	Z1	1.4 ± 0.47 (7)	-	-	-	-	2.6 ± 1.04 (5)	-	-	-	-
	Z2	0.9 ± 0.49 (21)	-	-	-	-	1.8 ± 0.51 (9)	-	-	-	-
	Z4	2.3 ± 0.90 (10)	1.6 ± 0.37 (4)	0.7 ± 0.29 (19)	0.8 ± 0.60 (21)	-	2.6 ± 0.67 (7)	1.5 ± 0.35 (2)	0.8 ± 0.27 (20)	2.0 ± 1.46 (6)	-
	R35[b]	2.0 ± 0.82 (14)	1.3 ± 0.84 (4)	0.9 ± 0.33 (13)	1.0 ± 0.71 (24)	1.6 ± 1.09 (34)	2.3 ± 1.00 (14)	1.7 ± 0.49 (3)	0.8 ± 0.26 (12)	1.2 ± 0.68 (20)	3.2 ± 3.18 (9)
	Z11	3.8 ± 1.62 (6)	1.6 ± 0.19 (3)	1.0 ± 0.36 (6)	-	-	2.7 ± 1.72 (11)	2.8 ± 0.44 (2)	1.1 ± 0.46 (5)	-	-
1996-97	Z6	1.7 ± 0.85 (17)	1.5 ± 0.61 (3)	1.1 ± 0.56 (3)	-	-	1.7 ± 0.80 (19)	1.3 ± 0.23 (4)	0.7 ± 0.79 (6)	-	-
	Z15	1.2 ± 0.87 (5)	-	-	-	-	1.2 ± 0.60 (4)	-	-	-	-
	I3	1.3 ± 0.43 (16)	1.8 ± 0.50 (3)	1.0 ± 0.36 (14)	1.2 ± 0.72 (24)	1.6 ± 0.90 (8)	2.9 ± 1.25 (8)	1.4 ± 0.36 (3)	0.8 ± 0.27 (15)	1.1 ± 0.75 (24)	5.7 ± 6.97 (7)
	I8	2.6 ± 1.0 (8)	-	-	-	-	1.9 ± 0.22 (8)	-	-	-	-
	V7	2.6 ± 0.81 (10)	1.7 ± 1.03 (3)	1.0 ± 0.00 (1)	-	-	2.3 ± 0.73 (12)	1.8 ± 0.32 (2)	0.9 ± 0.38 (3)	-	-
1997-98	V13	1.4 ± 0.70 (19)	2.2 ± 0.74 (2)	0.9 ± 0.56 (11)	0.8 ± 0.84 (13)	-	2.3 ± 1.11 (10)	3.6 ± 1.09 (2)	0.8 ± 0.67 (6)	1.2 ± 1.54 (10)	1.0 ± 0.97 (5)
	R35[c]	2.4 ± 0.50 (3)	-	-	-	-	3.5 ± 2.15 (2)	-	-	-	-
	Z10	2.5 ± 0.91 (10)	-	-	-	-	2.1 ± 1.00 (14)	-	-	-	-
	next Z9	4.5 ± 1.16 (4)	1.6 ± 0.20 (4)	0.9 ± 0.22 (16)	1.0 ± 0.55 (23)	2.3 ± 0.00 (1)	3.4 ± 0.95 (5)	2.1 ± 0.00 (1)	1.0 ± 0.33 (18)	1.3 ± 0.68 (22)	1.9 ± 1.38 (2)
	V3	3.0 ± 1.3 (7)	1.5 ± 0.00 (2)	1.1 ± 0.44 (13)	1.1 ± 0.87 (19)	-	2.5 ± 1.17 (10)	1.3 ± 0.66 (4)	0.8 ± 0.29 (17)	1.0 ± 0.84 (23)	-

[a] female deserted late chick-rearing; [b] female deserted late chick-rearing; [c] female deserted early incubation, male abandoned egg after incubating 32 days.

Appendix 5D: Shift durations at the nest for pairs of Shy albatrosses which were failed breeders during the 1995-96, 1996-97 or 1997-98 breeding seasons. Data are presented for each member of the pair, until the stage in which they failed, as the mean ± 1 SD, with the sample size given in parentheses. As failures occurred throughout the season overall means per stage were not calculated.

		Males			Females		
Year	Nest	Early Inc	Late Inc	Brooding	Early Inc	Late Inc	Brooding
	A1	3.0 ± 1.5 (6)	-	-	2.8 ± 1.94 (6)	-	-
	R21[a]	1.5 ± 0.67 (4)	0.9 ± 0.26 (4)	0.8 ± 0.41 (14)	2.4 ± 1.05 (11)	1.7 ± 0.68 (3)	0.9 ± 0.43 (15)
1995/96	Z1	3.8 ± 1.27 (4)	-	-	3.7 ± 1.38 (5)	-	-
	Z2	1.7 ± 1.47 (15)	-	-	3.6 ± 1.28 (9)	-	-
	Z4[b]	2.7 ± 0.62 (8)	1.8 ± 0.22 (3)	0.9 ± 0.18 (19)	3.4 ± 0.86 (8)	2.5 ± 0.80 (2)	0.7 ± 0.26 (20)
	R35[c]	3.4 ± 0.58 (10)	1.4 ± 0.72 (4)	0.8 ± 0.31 (13)	2.9 ± 0.79 (10)	1.8 ± 0.04 (3)	0.8 ± 0.30 (12)
	Z11[d]	5.3 ± 1.60 (6)	2.4 ± 0.55 (3)	0.9 ± 0.33 (4)	3.5 ± 1.70 (7)	1.4 ± 0.03 (2)	1.2 ± 0.25 (5)
1996-97	Z6[e]	3.1 ± 0.70 (13)	2.3 ± 0.64 (3)	2.3 ± 0.50 (3)	2.9 ± 0.52 (13)	2.3 ± 0.43 (4)	1.7 ± 0.00 (2)
	Z15	2.4 ± 0.72 (4)	-	-	2.7 ± 1.95 (3)	-	-
	I3	3.3 ± 1.11 (8)	1.6 ± 0.18 (2)	0.8 ± 0.32 (14)	3.6 ± 0.97 (8)	2.9 ± 0.82 (2)	1.0 ± 0.40 (14)
	I8	2.2 ± 0.35 (8)	-	-	2.9 ± 1.01 (9)	-	-
	V7[f]	3.3 ± 0.77 (10)	1.8 ± 0.32 (2)	1.6 ± 0.00 (1)	2.9 ± 0.82 (10)	2.9 ± 0.59 (2)	1.1 ± 0.32 (2)
1997-98	V13[g]	3.0 ± 1.48 (10)	2.9 ± 0.00 (1)	1.6 ± 0.72 (5)	4.0 ± 1.78 (8)	4.8 ± 0.18 (2)	2.1 ± 1.36 (5)
	R35[h]	13.4 ± 16.17 (3)	-	-	2.4 ± 0.46 (3)	-	-
	Z10	3.1 ± 1.35 (10)	-	-	2.7 ± 0.77 (10)	-	-
	next Z9[i]	4.3 ± 0.71 (4)	2.2 ± 0.00 (1)	1.2 ± 0.47 (16)	4.4 ± 1.10 (5)	5.3 ± 0.00 (1)	0.8 ± 0.32 (18)
	V3[j]	4.7 ± 1.64 (6)	3.1 ± 1.94 (2)	1.1 ± 0.35 (13)	3.7 ± 0.94 (6)	2.1 ± 0.68 (2)	1.1 ± 0.18 (13)

[a] female deserted/failed late chick-rearing; [b] failed early chick-rearing; [c] female deserted/failed late chick-rearing; [d] failed during brood; [e] failed during brood; [f] failed during brood; [g] failed late chick-rearing; [h] female deserted early incubation, male abandoned egg after incubating 32 days; [I] failed late chick-rearing; [j] failed early chick-rearing.

Appendix 5E: Foraging trip and shift durations (days) at the nest for both successful and failed breeders at Pedra Branca during the 1997/98 breeding season. Data are presented for each member of the breeding pairs up until the end of brooding, thereafter foraging trip and shift durations could be calcuated only for the individual carrying a transmitter.

Nest	Parameter	Bird with transmitter				Mate			
		Early Inc	Late Inc	Brooding	Late Chick	Early Inc	Late Inc	Brooding	Late Chick
					Successful breeders				
1	FT	3.2 ± 1.06 (2)	2.4 ± 0.00 (1)	1.3 ± 0.36 (3)	0.9 ± 0.43 (35)	5.0 ± 0.00 (1)	4.4 ± 2.50 (2)	0.9 ± 0.13 (3)	-
	Shift	3.8 ± 1.17 (2)	6.1 ± 0.00 (1)	0.9 ± 0.13 (3)	-	3.2 ± 1.06 (2)	2.0 ± 0.53 (2)	1.1 ± 0.08 (3)	-
2	FT	1.0 ± 0.59 (6)	0.8 ± 0.48 (4)	0.5 ± 0.03 (2)	2.1 ± 2.00 (18)	2.3 ± 0.92 (4)	2.7 ± 1.31 (4)	-	-
	Shift	2.9 ± 1.33 (4)	1.2 ± 0.17 (3)	-	-	1.8 ± 0.68 (4)	0.8 ± 0.49 (4)	-	-
3	FT	1.6 ± 0.78 (5)	1.3 ± 0.76 (3)	1.0 ± 0.71 (2)	1.5 ± 1.57 (22)	3.1 ± 0.35 (2)	2.5 ± 0.77 (3)	0.5 ± 0.00 (1)	-
	Shift	3.0 ± 0.29 (3)	2.1 ± 0.68 (2)	1.5 ± 1.38 (2)	-	2.8 ± 1.41 (3)	1.6 ± 0.23 (3)	0.5 ± 0.00 (1)	-
4	FT	1.6 ± 0.50 (3)	1.3 ± 0.52 (4)	0.8 ± 0.29 (4)	1.9 ± 1.03 (13)	2.4 ± 0.32 (2)	1.4 ± 0.90 (3)	1.4 ± 0.89 (4)	-
	Shift	2.4 ± 0.32 (2)	1.7 ± 1.01 (4)	1.1 ± 0.31 (4)	-	2.3 ± 0.53 (3)	1.1 ± 0.37 (3)	0.8 ± 0.29 (4)	-
5	FT	2.4 ± 0.59 (3)	-	-	2.1 ± 2.16 (15)	4.3 ± 1.54 (3)	-	-	-
	Shift	4.3 ± 1.54 (3)	-	-	-	2.4 ± 0.59 (3)	-	-	-
					Failed breeders				
6	FT	1.0 ± 0.31 (4)	-	-	-	5.0 ± 3.20 (3)	-	-	-
	Shift	5.0 ± 3.20 (3)	-	-	-	1.2 ± 0.88 (4)	-	-	-
7	FT	0.9 ± 0.59 (15)	-	-	-	2.2 ± 1.01 (7)	-	-	-
	Shift	1.9 ± 0.80 (8)	-	-	-	1.3 ± 0.49 (8)	-	-	-
8	FT	2.1 ± 0.84 (4)	1.3 ± 0.53 (2)	0.7 ± 0.00 (1)	-	3.8 ± 0.62 (2)	1.3 ± 0.23 (4)	0.8 ± 0.00 (1)	-
	Shift	2.8 ± 1.70 (3)	1.2 ± 0.27 (4)	0.5 ± 0.00 (1)	-	2.8 ± 0.76 (3)	1.3 ± 0.53 (4)	0.8 ± 0.00 (1)	-

Chapter 6

DIET OF SHY ALBATROSSES *Thalassarche cauta* AT ALBATROSS ISLAND, TASMANIA

6.1 INTRODUCTION

Albatrosses have recently been described as largely opportunistic feeders, the contributions of the major prey classes in their relatively catholic diet being reflected by the availability of accessible prey within the foraging zones (Cherel & Klages 1998). With their long wings, superbly adapted for gliding flight, albatrosses were long thought to obtain their prey solely from the sea surface. While the large Wandering *Diomedea exulans* and Royal *D. epomophora* albatrosses appear restricted to foraging in this manner, the diving capabilities of the smaller albatross species indicate that they can access prey in excess of 10 m depth (Prince et al. 1994, Hedd et al. 1997, Huin & Prince 1997). The diets of albatrosses are dominated by cephalopods, fish, and to a lesser extent, crustaceans, while carrion and gelatinous zooplankton tend to be minor components (Cherel & Klages 1998).

At a time when anthropogenic influences are increasingly impacting both individual albatrosses and influencing trends in population size (Croxall et al. 1998, Gales 1998, Weimerskirch & Jouventin 1998), information on the diet and foraging ecology of these predators remains scarce. This information is urgently required in order to circumvent, or at least minimize, further detrimental interactions with human activities. Of the 24 albatross species (Robertson & Nunn 1998), Shy albatrosses *Thalassarche cauta* are medium sized (3.5-5.0 kg) and endemic to Australia, breeding in three colonies off the coast of Tasmania. Whilst the juveniles may traverse the Southern Oceans (Brothers et al. 1997), adults are relatively sedentary, during both the breeding and non-breeding periods and they are distributed at sea over the continental shelf and shelf slope waters off southeast Australia (Brothers et al. 1997, 1998, and Chapters 3 & 8). This restricted distribution makes the resident population of approximately 12,250 breeding pairs (N. Brothers, unpubl. data) significant consumers of marine resources within the Tasmanian region. The waters around Tasmania are also heavily utilized fishing grounds, with substantial effort in the Southeast trawl, the Southern Rock lobster *Jasus edwardsii*, and the various Finfish fisheries. Combined with their prevalence as by-catch in both foreign

and Australian domestic longline fisheries for Southern Bluefin tuna *Thunnus maccoyii* (Gales et al. 1998, Brothers & Foster in press), the restricted distribution of Shy albatrosses also makes them particularly vulnerable to commercial exploitation of their main prey species.

There have been no detailed quantitative studies of the diet of Shy albatrosses in the Tasmanian region. To date, the only published information comes from a single collection described by Green (1974). Of 75 regurgitate samples collected from chicks at Albatross Island (western Bass Strait), fish were present in 59% of the samples, cephalopods in 51% of the samples, followed by crustaceans and tunicates, which were found in 35% and 32% of the samples, respectively. This study augments the dietary information for the species by presenting data collected over four consecutive breeding seasons (1994/95 to 1997/98) at Albatross Island. During the first two seasons the diet sampling was largely opportunistic. Full stomachs were dissected from chicks that had died from viral infections, and spontaneous regurgitations were collected from chicks at banding. During 1996/97 and 1997/98 such collections were augmented by systematically sampling the fresh food delivered to chicks by their parents. Together these samples were used to:

- determine the relative contribution of the major prey classes to the composition of the diet during the chick-rearing period, and to quantify inter- and intra-annual variation;
- produce a comprehensive list of the prey species delivered to chicks;
- estimate both the sizes of the prey consumed, and the sizes of meals chicks received;
- compare estimates of diet composition obtained from opportunistic and more systematic sampling regimes;
- estimate the relative contribution of materials scavenged as offal, bait or fisheries discards to the composition of the diet.

6.2 METHODS AND MATERIALS

6.2.1 *Species and study site*

Recent revisions to albatross taxonomy have elevated the Shy albatrosses breeding in

Australia to full species status (Nunn et al. 1996, Robertson & Nunn 1998). Breeding occurs at three locations, Albatross Island (40° 24'S, 144° 32'E) in western Bass Strait, and Pedra Branca (43° 52'S, 146° 58'E) and Mewstone (43.742°S, 146.375°E) off Tasmania's south coast. The albatrosses breed annually at these sites, and eggs are laid in September. Incubation lasts for approximately 10 weeks (N. Brothers, unpubl. data), with eggs hatching in early December. Young chicks are brooded in alternate shifts by their parents over the next 27 days (Chapter 5, and N. Brothers, unpubl. data), prior to being left alone at the nest. Parents forage both for themselves and their single chick over the next 14-16 weeks, and fledging typically occurs in April.

6.2.2 *Field sampling protocol*

Most (>99%) of the diet samples were collected from chicks at Albatross Island (between December and April) between 1994/95 and 1997/98, while a total of 5 samples which were thought to contain "unusual" prey items were collected from fledging-aged chicks at Pedra Branca in 1995/96 and 1996/97.

Three types of diet samples were collected;

- *whole stomachs* - whole stomachs (including contents of the proventriculus and ventriculus) were collected from chicks that died of viral infections at Albatross Island;
- *incidental chick regurgitations* - spontaneous regurgitations (containing partial contents of the proventriculus) were collected from live chicks handled for banding;
- *fresh food samples* - following observed feeds from their parents, the stomach contents of chicks were collected by inverting them over a plastic bucket. These samples would also have contained partial contents of the proventriculus.

During visits to Albatross Island, whole stomachs were sampled from chicks during three stages of each breeding season, which roughly corresponded to early (2-4 wk old chicks, late December-early January), mid (8-10 wk old chicks, early-mid February) and late chick-rearing (16-18 wk old chicks, early-mid April). The study commenced at fledging in 1994/95, and as such, only one set of samples was collected that season. In all periods, whole stomachs were collected from chicks that recently died from viral infections. A lethal avian pox virus, transmitted via fleas and ticks, is prevalent at Albatross Island. Repeated infection of the virus causes death from liver and kidney failure. While the extent of impact of the virus can vary widely between years, breeding productivity is

reduced to as little as 10% in some colonies in some years (N. Brothers, unpubl. data).

At Albatross Island, all colonies were checked every 1-2 days for fresh dead chicks. Chicks were removed from the colony, and prior to dissection they were weighed to the nearest 50 g using a 10 kg Salter spring balance and morphometric measurements were taken. Upon dissection, carcasses were assigned a qualitative condition score (ranging from 0 to 5) based upon their relative quantity of fat (a score of 0 indicated an absence of fat, while 5 indicated that the chick had substantial interstitial and peritoneal fat reserves). Complete stomach contents (including contents of the proventriculus and ventriculus) were ensured through removal of the intestinal tract from the esophagus to the point of articulation of the small intestine. In the field, samples were stored separately in plastic bags containing 70% ethanol, and upon return to Hobart they were frozen at -20° C until further analysis.

As a spontaneous defense mechanism, Shy albatross chicks regularly eject their stomach contents when approached. A small number of these incidental regurgitations were collected from chicks handled during banding at both Albatross Island and Pedra Branca. Results for Pedra Branca are presented separately. As just a small number of these samples were collected at Albatross Island, they were pooled along with the whole stomach samples for all analyses.

During 1996/97 and 1997/98, fresh food samples were collected from live chicks at Albatross Island during mid and late chick-rearing. After a parent had been observed to feed it's chick and depart the colony, the chick was quickly and quietly approached and inverted over a plastic bucket. Stomach contents were obtained by gently massaging the chicks abdomen and throat until food was no longer ejected. Chicks were immediately replaced on their nests, and the nests marked both to ensure that they were sampled only once, and to monitor the effects of the meal loss on their fledging prospects. The proportion of chicks sampled at mid-chick-rearing that were alive, dead or assumed to have already fledged from the colony were compared with proportions in a control plot. As field trips were brief and chicks mobile at fledging, there was no further monitoring of the chicks sampled during this period.

Fresh food samples were weighed to the nearest 10 g using a Pesola 1 kg spring balance. As it was not practical to immediately freeze samples in the field, they were sorted and stored in order to arrest further digestion. Whole samples were placed in a fine sieve to drain, generally overnight, and the solid and liquid portions of the meals were separated. Each component was then reweighed. Liquid portions were stored unpreserved in plastic

bags, while the solid portions were placed in plastic bags along with 70% ethanol. Upon return to Hobart, samples were frozen at -20° C until sorted.

6.2.3 *Sample processing and data analysis*

All samples were thawed and drained of ethanol prior to sorting. Whole stomachs were dissected and their contents flushed into a series of stacked sieves (smallest 0.5 mm) using running water. Each broad prey class (eg, cephalopod, fish, crustacean and tunicate) was separated, and whenever possible the number of prey items of each species was counted. Numbers of cephalopods were estimated from lower mandibles (beaks), numbers of crustaceans either from whole individuals or from pairs of eyes (for krill), and the numbers of fish from pairs of otoliths, jaws, opercula or sections of caudal vertebrae. Whenever fish consumption was obvious from sections of vertebrae or other bones, without accompanying diagnostic remains, the number of fish was arbitrarily estimated to be one. Results were expressed as frequency of occurrence and percent number for each taxon (Hyslop 1980, Duffy & Jackson 1986). As most prey recovered from whole stomachs were accumulated, and given the problems associated with differential retention and voiding of prey remains (Pierce & Boyle 1991; Gales et al. 1993), no attempt was made to estimate contribution by mass for these samples.

Almost without exception, whole stomachs from the dead chicks contained only accumulated items (primarily loose or eroded cephalopod beaks, eroded fish otoliths or vertebrae, and stones). In contrast, the fresh food samples contained mainly fresh prey, and they therefore required a modified sorting procedure. Solid portions were suspended upright and their preservative drained overnight by gravity through tiny perforations made in the plastic bags. The resulting solid portion was re-weighed using a top loading balance, accurate to the nearest 0.1 gram, and then placed into a sorting tray. All accumulated items were removed and weighed, leaving only the fresh prey. These were separated into broad prey classes (fish, squid, crustaceans, tunicates) and weighed, again to the nearest 0.1 g. Following storage in ethanol the solid masses of these samples averaged 21 ± 40.0% (range -53-96%) lower than the masses recorded in the field. Despite this, the contributions of the major prey classes to sample wet mass were calculated assuming that their relative proportions were the same as they were prior to storage in ethanol. Differences in sample mass were perhaps largely attributable to differences in the resolution of the scales used in the field (± 10g) and in the lab (± 0.1 g), especially for the small samples (≤ 50 g), but differences also likely resulted from dehydration of the prey whilst stored in ethanol. For each species identified within the

major prey classes, the number of individuals was counted, as described for the stomach samples. The fresh portions of these samples were expressed as percent frequency of occurrence, percent numerical abundance, and percent by wet mass (Hyslop 1980, Duffy & Jackson 1986).

Cephalopod mandibles were stored in dilute ethanol (10%), while crustaceans and tunicates were stored in concentrated (70%) ethanol. Fish remains (otoliths and other bones) were stored dry. Whenever intact, individual fish and squid items were measured and weighed. Alternatively, uneroded diagnostic remains were used to estimate the sizes of the prey consumed. For cephalopods, lower rostral lengths (LRL), hood lengths (HL) or crest lengths (CL) were measured to the nearest 0.1 mm using vernier calipers or a dissecting microscope fitted with a graticule, and regression equations from the literature were used to estimate the dorsal mantle length (DML) and wet weight of cephalopods eaten. The sizes of fish consumed were estimated by measuring the length of otoliths that were either extracted from fish skulls or found loose in the samples, but showing no sign of erosion. Otoliths were measured (to the nearest 0.1 mm) using a dissecting microscope fitted with a graticule. Fish sizes were estimated using published regressions of otolith length again fork length and mass. Conversion formulae used for estimating the sizes of the prey consumed, along with the source references are provided in Appendix 6A.

Cephalopod identifications were made through comparison with a reference collection held by Parks and Wildlife Service, Hobart, Australia (complied by R. Gales, and reviewed by M.R. Clarke and C.C. Lu), and through direct consultation with N. Klages (Port Elizabeth Museum, South Africa). Identification of fish from otoliths was made with comparison to collections held by Parks and Wildlife Service, Hobart, Australia (complied by R. Gales), and CSIRO, Hobart, Australia (compiled by D. Furlani) while identification of fish from other diagnostic remains were made with the help of A. Graham (CSIRO, Hobart, Australia). Crustacean and tunicate identifications were made by D. Ritz (University of Tasmania, Hobart, Australia).

6.2.4 *Allocation of prey species to discard/by-catch status*

An estimate was made of the contribution of trawler discards/by-catch to the albatrosses diet composition. Fish species were considered to have been made available by trawlers if they were deepwater species and/or they were known to be taken as trawler by-catch within Tasmanian waters (detailed by Last et al. 1983). Given the fish species consumed, allocation was relatively straightforward. The situation, however, was less clear for cephalopods. Allocations were based both upon the habits of the squid and upon the

information presented by Lipinski & Jackson (1989) regarding squid Families which were known to "float or sink" after death. This information allowed an assessment of the feasibility of the albatrosses naturally foraging either upon live, moribund or dead squid near the surface. In the absence of information on floating/sinking status, assumptions were made in favour of trawler-related availability.

Ethical approval for this work was granted by the University of Tasmania's Animal Ethics Committee (Project 95057) and permission to work on Albatross Island was granted by the Tasmanian Department of Environment and Land Management (Permit numbers. FA 95290, FA 96093 and FA 97048). Results are presented as mean ± 1 SD throughout, and a $p < 0.05$ was taken to indicate that the results were statistically significant.

6.3 RESULTS

6.3.1 *Sample size and description*

In total, 657 diet samples were collected; 652 from Albatross Island and five from Pedra Branca. At Albatross Island, 83% (540) of the samples were whole stomachs from fresh dead chicks, 2% (16) were incidental regurgitations collected from live chicks at banding, while the remaining 15% (96) were fresh food samples collected from recently fed chicks (Table 6.1). At Pedra Branca five partial incidental regurgitations were collected from live chicks at banding (Table 6.1). While most samples (90%) contained identifiable prey, the tendency for hard parts to accumulate through time resulted in the whole stomach samples collected between mid and late chick-rearing being slightly more likely to contain prey than those collected from young chicks (2-4 weeks) in December (Table 6.1).

6.3.2 *Effect of fresh food collections on fledging success*

Collection of a single regurgitate sample during the middle of the chick-rearing period had no discernible effect on chick survival to fledging, with similar proportions of live (75% vs 74% in 1997/97 and 64% vs 78.6% in 1997/98) and dead (8.3% vs 7.4% in 1996/97 and 8.0% vs 9.5% in 1997/98) chicks in the study and control plots at fledging each year (χ^2=0.094, df=1, $p > 0.05$ in 1996/97, and χ^2=2.94, df=1, $p > 0.05$ in 1997/98, respectively). Adding the proportion of empty nests (those from which chicks were assumed to have already fledged), study and control plots were similar in 1996/97 (χ^2=0.23, df=2, $p > 0.05$), but significantly different in 1997/98 (χ^2=24.74, df=2, $p <$

0.01). In 1997/98, however, the result was opposite to what would have intuitively been expected if the sampling negatively impacted chick survival, as a higher proportion of the sampled chicks were assumed to have already fledged (28% vs 12%).

Table 6.1: Description and number of diet samples collected from Shy albatross chicks from Albatross Island (AI) and Pedra Branca (PB), Tasmania between April 1995 and April 1998.

Sampling period	Site	Chick age (weeks)	Sample type	Number of samples collected	Samples with identifiable prey	
					n	%
April 1995	AI	16-18	whole stomachs	47	47	100
	AI	16-18	incidental regurgitations	13	11	85
	PB	16-18	incidental regurgitations	3	3	100
December 1995	AI	2-4	whole stomachs	16	9	56
February 1996	AI	8-10	whole stomachs	90	84	93
April 1996	AI	16-18	whole stomachs	101	99	98
	AI	16-18	incidental regurgitations	3	2	67
	PB	16-18	incidental regurgitations	2	2	100
December 1996	AI	2-4	whole stomachs	37	22	59
February 1997	AI	8-10	whole stomachs	61	53	87
	AI	8-10	fresh food	24	23	96
April 1997	AI	16-18	whole stomachs	64	57	89
	AI	16-18	fresh food	22	16	73
January 1998	AI	3-5	whole stomachs	19	18	95
February 1998	AI	9-11	whole stomachs	55	55	100
	AI	9-11	fresh food	25	21	84
April 1998	AI	16-18	whole stomachs	50	48	96
	AI	16-18	fresh food	25	21	84
Total				657	591	90%

6.3.3 *General composition of the diet samples*

6.3.3.1 *Frequency of occurrence*

Fish was the most important prey type in terms of frequency of occurrence (FOO%) in the fresh food samples (Table 6.2), being present in more than 90% of the samples during each of the sampling sessions (Figure 6.1a). Cephalopods were also an important prey group (Table 6.2 and Figure 6.1a), but they showed more variability in occurrence through time, being present in between 14 to 52% of the samples. Crustaceans were important in terms of frequency of occurrence only in February 1997, when they occurred in 45% of samples. In other sessions they occurred in less than 5% of the samples. The occurrence of tunicates also varied temporally, generally occurring more frequently in

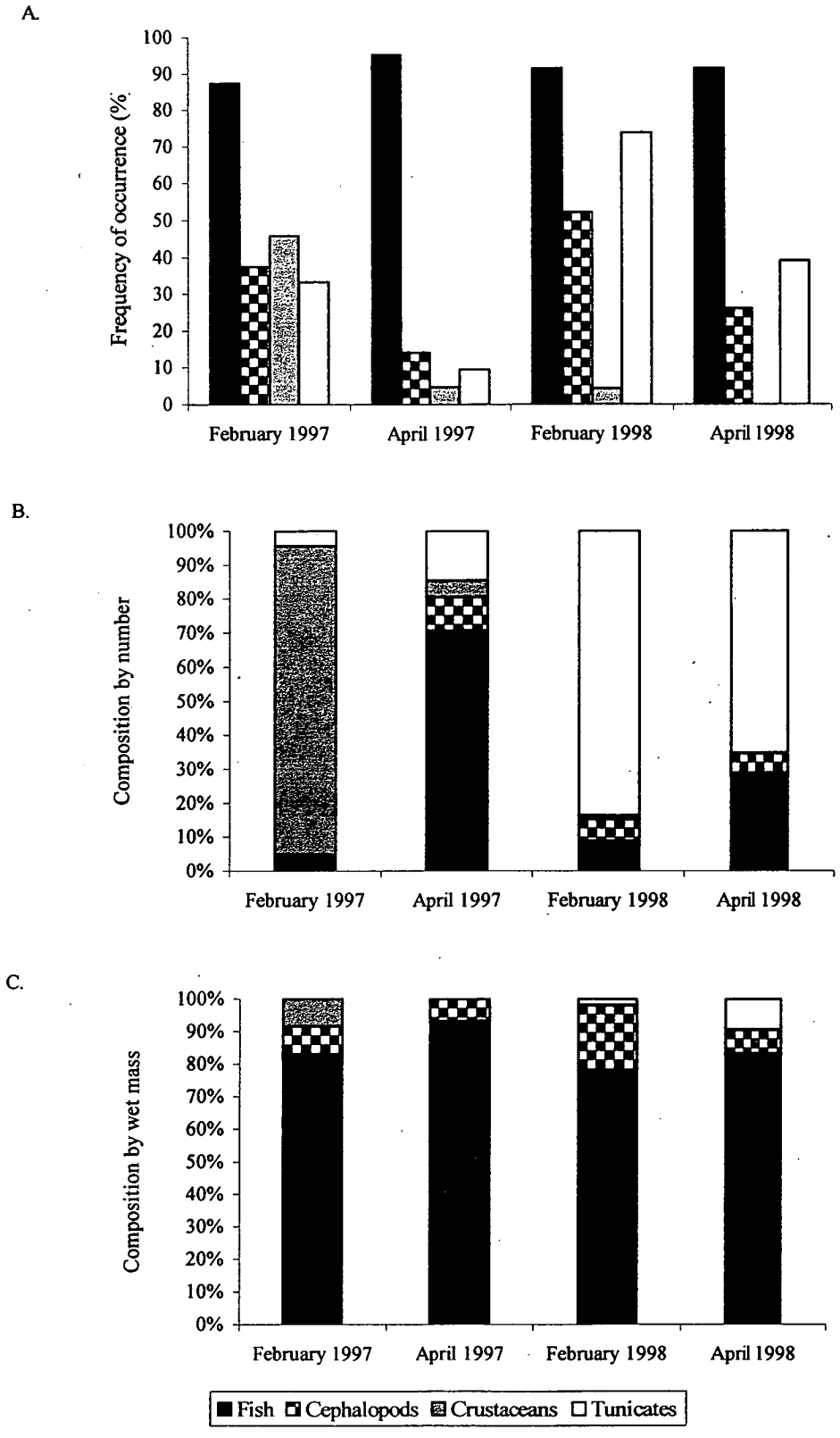


Figure 6.1: General composition of the fresh food samples taken from Shy albatross chicks at Albatross Island expressed as (A) percent frequency of occurrence, (B) percent by number, and (C) percent by wet mass for the four major prey classes.

February than in April, and overall they were more common in 1998 than 1997 (Table 6.2 and Figure 6.1a).

The relative frequency of occurrence of the major prey taxa when assessed from whole stomachs was markedly different (Table 6.2 and Figures 6.1a and 6.2a). Cephalopods were the most frequently occurring prey type in these samples, and their predominance was consistent during all sampling sessions (Figure 6.2a). Fish were also an important prey group, but presumably because fish remains are less resistant to digestion than cephalopod remains, they were always present in less than 55% of the samples. Tunicates occurred frequently, but similar to the fresh food samples, their occurrence varied through time. During February and April of 1996, and during all sampling sessions in 1998 they occurred in more than 50% of the samples (Figure 6.2a). With the exception of stomachs from young chicks in December of 1995 and 1996, crustaceans occurred infrequently.

Seabird remains were of negligible importance, and in the one sample that contained more than a single feather, they were identified as belonging to a Common Diving petrel (*Pelecanoides urinatrix*, identified by N. Brothers). Five (0.9%) of the whole stomach samples contained small pieces of plastic, and these ranged from segments of clear plastic bags to fragments of hard plastic (cream and red in colour). None of the fresh food samples contained foreign matter.

Table 6.2: Frequency of occurrence and percent by number for the major prey taxa in Shy albatross diet samples containing prey.

	Fresh food samples	Whole stomachs & incidental regurgitations
Frequency of occurrence (%)	n=91	n=540
Fish	92	25
Cephalopods	33	95
Crustaceans	14	6
Tunicates	40	56
Composition by number (%)	n=1,556	n=10,645
Fish	9	2
Cephalopods	3	35
Crustaceans	63	3
Tunicates	26	61

6.3.3.2 *Composition by number*

The contribution of the major prey classes to the composition by number of the fresh food

samples varied substantially through time (Figure 6.1b). Crustaceans predominated by number in February 1997, fish predominated in April 1997, and tunicates predominated during both sampling periods in 1998. The number of prey items per sample varied through time (one-way ANOVA, on log total prey per sample, $F_{3,87}=8.13$, $p < 0.001$), being highest in February 1997 (44 ± 156.2 items per sample) when 773 Australian krill *Nyctiphanes australis* (71% of the total prey items during this period) were recovered from a single sample (Table 6.3). The number of prey per sample was also high during 1998, when large numbers of salps (*Pyrosomas spp.*) were found in the diet. While large numbers of krill and salps were present in some samples, these prey contributed little to wet mass (Figure 6.1c), and likely also contributed little in terms of energy density. Considering just the fish and squid components of the diet, which together always contributed more than 92% to sample wet mass, the number of prey items per sample was low, and consistent between years ($F_{1,85}=0.000$, $p=0.933$, 2 ± 1.3 items per sample in both 1996/97 and 1997/98, Table 6.3). The number of prey per sample, however, differed according to time of year, with samples collected in February containing more prey items than those collected at fledging in April ($F_{1,85}=6.49$, $p=0.013$, 2.4 ± 1.35 vs 1.6 ± 1.08 items, respectively, Table 6.3). While numerous small prey items strongly influenced the diet composition in terms of percentage by number, the bulk of the diet (in terms of wet mass) was comprised of few relatively large fish and squid prey.

Table 6.3: Mean number of prey items recovered per sample from the fresh food samples containing prey. Data are presented for all prey classes as well as when restricted to the fish and squid components of the diet.

	Number of prey per sample	
Sampling period	Total prey	Fish & squid components
February 1997	44.7 ± 156.2 (1 - 773)	2.5 ± 1.4 (1 - 6)
April 1997	2.0 ± 1.8 (1 - 7)	1.6 ± 1.0 (1 - 4)
February 1998	14.8 ± 20.8 (1 - 78)	2.3 ± 1.3 (1 - 6)
April 1998	4.5 ± 6.5 (1 - 31)	1.7 ± 1.2 (1 - 6)
Pooled	17.1 ± 81.55 (1 - 773)	1.9 ± 1.31 (1 - 6)

The prey class predominating whole stomachs, in terms of numbers, also varied through time (Figure 6.2b). Cephalopods predominated during most periods, except in December 1996 when crustaceans were most abundant, and throughout 1998 when tunicates accounted for over 60% of the prey items recovered in all sessions. At Albatross Island, there were differences between years and stages of the breeding season in the number of prey items recovered from whole stomachs (two-way ANOVA on log transformed data,

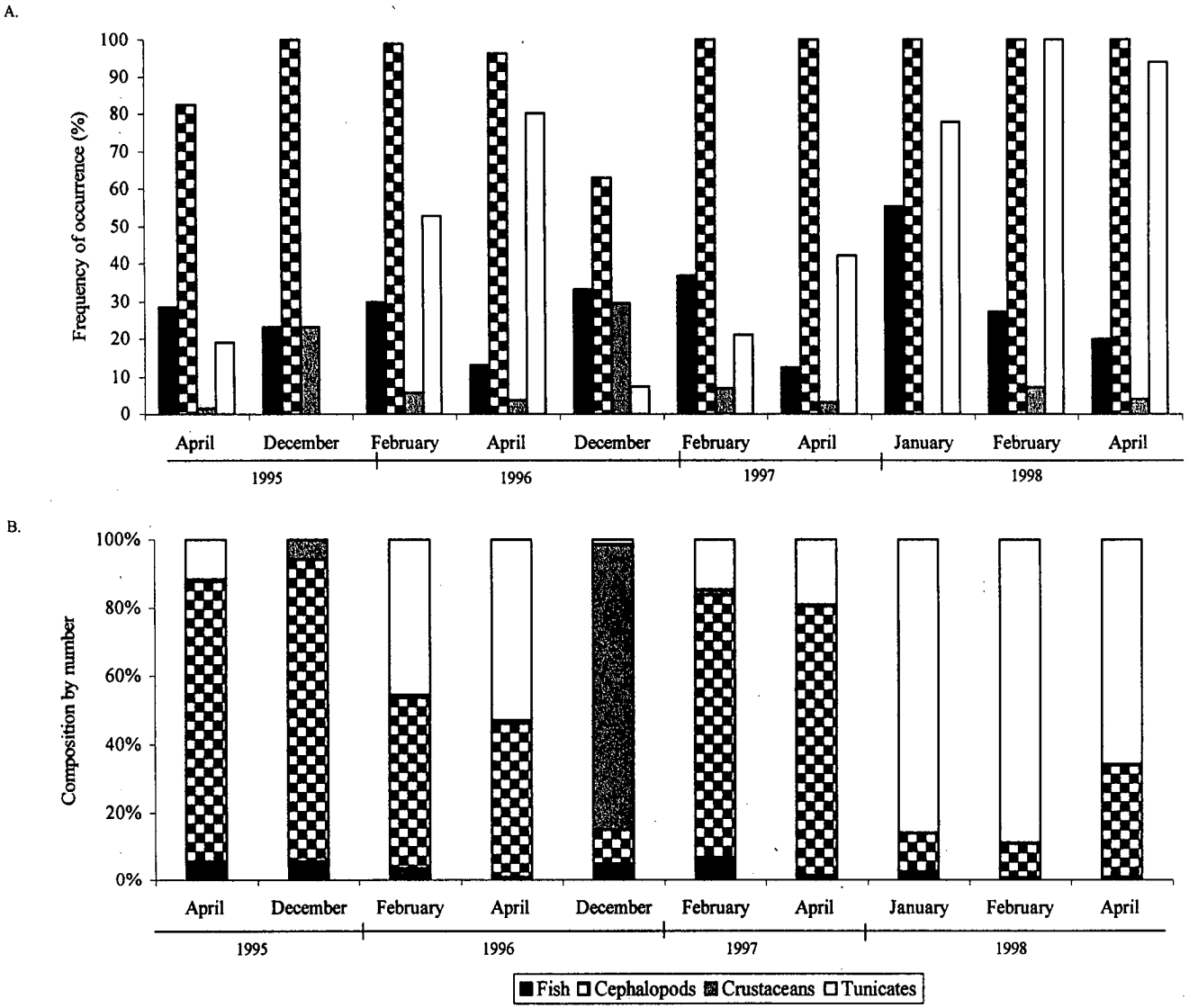


Figure 6.2: General composition of the opportunistic diet samples collected from Shy albatross chicks at Albatross Island expressed as (A) percent frequency of occurrence and (B) percent numerical abundance for the four major prey classes.

$F_{2,468}$=91.32, $p < 0.001$, $F_{2,468}$=34.20, $p < 0.001$, respectively), with significantly more prey items recovered per stomach in 1997/98 (48 ± 100.1) than in 1995/96 or 1996/97 (13 ± 12.1 and 8 ± 16.9), and in 1995/96 stomachs also contained more prey items than in 1996/97 (Tukey's HSD, $p < 0.01$ for all comparisons; Table 6.4). Inter-annual differences resulted, in part, from high numbers of salps recovered during 1997/98. Given the abundance of squid during most sampling periods, inter and intra-annual comparisons of the number of prey items per in whole stomach samples were also made separately for this class. The number of squid per stomach also varied within and between years (two-way ANOVA on log transformed data, $F_{2,453}$=61.68, $p < 0.001$, $F_{2,453}$=15.15, $p< 0.001$, respectively). Significantly more squid were recovered per stomach during 1995/96 and 1997/98 (6.5 ± 3.92 and 8.2 ± 5.35) than in 1996/97 (5.7 ± 3.83, Tukey's HSD, $p < 0.01$). There was also an increase in the number of squid beaks recovered per stomach throughout the breeding season, with beaks accumulating progressively from brood, to mid-chick-rearing and fledging (3.4 ± 2.81, 5.4 ± 3.74, 8.6 ± 4.45, respectively, Tukey's HSD $p < 0.001$ for all comparisons).

Table 6.4: Mean number of prey items recovered per sample from the whole stomachs that contained prey. Data are presented for all prey classes as well as when restricted solely to the squid component of the diet.

	Number of prey per sample	
Sampling period	Total prey	Squid component
April 1995	11.6 ± 8.8 (1 - 38)	11.5 ± 7.0 (1 - 31)
December 1995	5.3 ± 4.1 (1 - 13)	4.7 ± 3.1 (1 - 10)
February 1996	9.6 ± 11.3 (1 - 80)	5.0 ± 3.2 (1 - 13)
April 1996	17.9 ± 11.8 (1 - 71)	8.1 ± 4.0 (1 - 19)
December 1996	9.9 ± 38.5 (1 202)	1.6 ± 1.0 (1 - 4)
February 1997	6.2 ± 3.7 (1 - 18)	4.8 ± 3.2 (1 - 18)
April 1997	9.6 ± 5.7 (1 - 29)	7.6 ± 3.7 (1 - 17)
January 1998	37.2 ± 86.4 (1 - 367)	4.3 ± 2.9 (1 - 10)
February 1998	65.5 ± 139.2 (2 - 922)	6.8 ± 4.7 (1 - 25)
April 1998	33.4 ± 19.4 (1 - 85)	11.1 ± 5.3 (1 - 21)

6.3.3.3 *Composition by wet mass*

During all periods, fish dominated the wet mass of the fresh food samples (Figure 6.1c and Table 6.5), with fish accounting for 78 to 93% of sample wet mass. Cephalopods were the second most important class of prey consumed, and they contributed between 7 and 20% by mass. Crustaceans and salps always contributed little to wet mass.

Table 6.5 Percentage by wet mass (mean ± S.D., (range)) of the major prey taxa present in solid portions of the fresh food samples from Shy albatross chicks at Albatross Island 1996/97, 1997/98 and when pooled across years.

Prey taxa	February 1997 n=24	April 1997 n=22	February 1998 n=25	April 1998 n=25	Pooled n=96
Fish	83.1 ± 32.81 (0.0 - 100.0)	93.2 ± 22.44 (0.0 - 100.0)	78.1 ± 35.25 (0.0 - 100.0)	83.1 ± 29.87 (0.0 - 100.0)	83.6 ± 30.66 (0.0 - 100.0)
Cephalopods	8.6 ± 20.64 (0.0 - 77.2)	6.8 ± 22.46 (0.0 - 100.0)	19.8 ± 34.62 (0.0 - 96.4)	7.4 ± 14.68 (0.0 - 44.5)	11.0 ± 24.12 (0.0 - 100.0)
Crustaceans	8.4 ± 28.20 (0.0 - 100.0)	0.0 ± 0.18 (0.0 - 0.8)	0.0 ± 0.02 (0.0 - 0.1)	- -	2.2 ± 14.66 (0.0 - 100.0)
Tunicates	0.1 ± 0.26 (0.1 - 1.1)	0.0 ± 0.08 (0.0 - 0.3)	2.0 ± 3.17 (0.0 - 11.5)	9.5 ± 28.60 (0.0 - 100.0)	3.0 ± 14.67) (0.0 - 100.0)

6.3.4 *Detailed composition of the diet*

6.3.4.1 *Description of the fresh food samples*

The mean mass of the food samples collected from Shy albatross chicks along with the percent contribution of the solid and liquid constituents are provided in Table 6.6. The total mass of food samples was similar in 1996/97 and 1997/98 ($F_{1,92}$=0.03, p=0.860), but the masses differed according to sampling period, with samples collected in February being heavier than those collected in April (530 ± 259.6 vs. 394 ± 260.1 g, $F_{1,92}$=6.42, p=0.013). The mass of the solid fraction was similar during February and April ($F_{1,92}$=1.83, p=0.180), and similar between years ($F_{1,92}$=1.18, p=0.280), while the liquid fraction was both greater in February than April (245 ± 129.2 vs. 160 ± 116.8 g, $F_{1,92}$=12.06, p=0.001), and greater in 1997/98 than in 1996/97 (226 ± 128.1 vs. 179 ± 128.5 g, $F_{1,92}$=3.93, p=0.050).

6.3.4.2 *Meal sizes vs. size of fresh food samples*

In a concurrent study of chick provisioning and growth (Chapter 7) the sizes of meals delivered to chicks were recorded throughout the rearing period using a series of automatic weighing platforms (Francis Scientific Instruments, Bourne, Cambridge, UK). The masses of these meals were compared with the masses of the fresh food samples collected concurrently. In February 1997 masses were significantly different, with the fresh food samples weighing more (521 ± 269.1 g vs 342 ± 178.5 g, t=2.58, df=40, p=0.007, Table 6.6). Chicks are provisioned at a higher rate in February than at fledging (in April, Chapter 7), and it seems likely that both the higher total mass of the fresh food samples, as well as and the greater overall proportion of liquid in the samples from

February originated from the breakdown of previous meals. These differences, however, would apparently not be consistent through time, as the mass of the fresh food samples and meals collected during February 1998 were similar (539 ± 255 g vs. 449 ± 188.7 g, t=1.25, df=34, p=0.109, Table 6.6). There was insufficient data to compare the sizes of fresh food samples and meals during April of either year.

Table 6.6 Solid and liquid constituents (mean ± S.D., (range)) of the fresh food samples collected from Shy albatross chicks at Albatross Island, 1996/97 and 1997/98. Measures were those obtained in the field, prior to storage in ethanol. The masses of single meals delivered to chicks during the same periods are also given.

Parameter	February 1997 n=24	April 1997 n=22	February 1998 n=25	April 1998 n=25
Total mass (g)	521 ± 269.1 (150 - 1085)	394 ± 257.4 (35 - 980)	539 ± 255.4 (50 - 1060)	394 ± 267.8 (35 - 1060)
Solid mass (g)	292 ± 193.7 (15 - 655)	262 ± 183.8 (0 - 610)	279 ± 156.0 (0 - 570)	203 ± 190.4 (0 - 670)
Liquid mass (g)	229 ± 136.1 (20 - 620)	132 ± 88.6 (20 - 370)	260 ± 123.1 (50 - 515)	192 ± 126.1 (35 - 475)
% Solid	52 ± 17.9% (16 - 77)	60 ± 20.7% (0 - 80)	47 ± 18.8% (0 - 67)	43 ± 26.0% (0 - 81)
% Liquid	48 ± 17.9% (15 - 83)	40 ± 20.7% (23 - 100)	53 ± 18.8% (32 - 100)	57 ± 26.0% (19 - 100)
Meal size (g)	342 ± 178.5 (n=18)	-	449 ± 188.7 (n=14)	-

6.3.4.3 *Numbers of prey items*

A total of 1,556 fresh prey items were counted in the fresh food samples, and 1,493 (96.0%) of these were sufficiently intact to be identified to species or Family level. From the chick stomachs, a total of 10,645 prey items were counted, and of these, 8,565 (80.5%) were identified to either species or Family level. The species composition of the fresh food samples, and the whole stomachs and incidental regurgitations (combined), in terms of both frequency of occurrence and percent numerical abundance, are given in Appendix 6B and Appendix 6C, for each sampling session.

6.3.4.4 *Samples from Pedra Branca*

The species composition of the samples collected from Pedra Branca are presented in Table 6.7. A total of 18 prey items were collected and all were identified to species or Family level. Two fish were amongst the prey items, the Southern whiptail *Coelorinchus australis* and a Merlucciid spp. (Table 6.7), along with two cephalopods, Gould's squid

and the deepwater squid *Moroteuthis ingens*. The remaining 13 prey items were crustaceans. Eleven barnacles *Lepadomorpha* were identified, along with an isopod, and a burrowing lobster from the Family *Scyllarridae*.

Table 6.7: Numbers of the various prey types recovered in the diet samples collected from Pedra Branca. ** Indicates deepwater species which may have been taken as trawler discards/by-catch.

	March/April 1995	March/April 1996
Fish		
Macrouridae		
Southern whiptail (*Coelorinchus australis*) **	1	-
Merlucciidae	1	-
Cephalopods		
Gould's squid (*Nototodarus gouldi*)	2	-
Moroteuthis ingens **	1	-
Crustaceans		
Cirripedia		
Barnacle spp. (*Lepadomorpha*)	2	9
Isopoda	1	-
Decapoda		
*Scyllarridae***	-	1

6.3.4.5 *Fish*

6.3.4.5.1 Fresh food samples

Of the 133 fish counted, 87 (65.4%) were identified either to species or Family level (Appendix 6B). Of the unidentified fish, intact otoliths were recovered from three individuals (2.3%) but they could not be identified, while for the remainder either no diagnostic remains were present or they were present but too eroded to identify (32.3%, Appendix 6B). Six species were identified, and a further three types were identified to Family level. In terms of both frequency of occurrence and percent numerical abundance, Jack mackerel *Trachurus declivis* dominated the fish component of the diet, occurring in 54% of the samples and accounting for 64% of all identified fish (Table 6.8). The importance of Jack mackerel was relatively consistent throughout all sampling sessions (Figure 6.3), where this species accounted for 50 to 80% of all fish identified. In both February 1997 and April 1998 Redbait *Emmelichthys nitidus* also contributed significantly to the diet, accounting for between 20 and 36% of the fish eaten (Figure 6.3). The contribution of this species, however, was not consistent through time, with no Redbait recorded in the other sampling periods (Appendix 6B and Figure 6.3). The only other fish prey type constituting more than 5% by number of the fish eaten, or

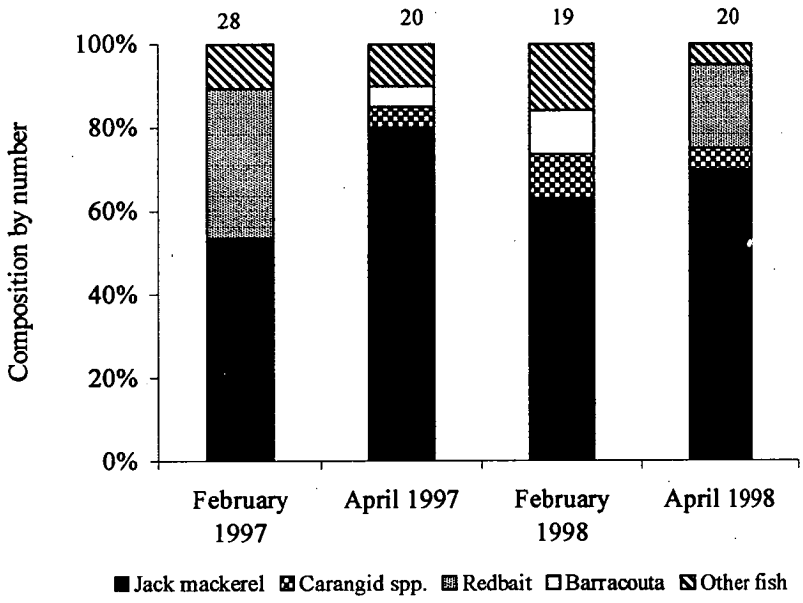


Figure 6.3: Contribution by number of the fish species present in fresh food samples during each sampling period. Species were included where they constituted ≥ 10% of the number of fish consumed in any one period.

occurring in more than 5% of the samples, was Carangid spp. (Table 6.8). In the absence of otoliths, this prey type was identified from the presence of lateral line scutes in the samples. Within the foraging zones of the albatrosses at this site, the Family Carangidae is represented by Jack mackerel and Silver trevally *Pseudocaranax dentex* (Last et al. 1983). In an uneroded state the lateral line scutes could be used to distinguish these species, but this was impossible when the scutes were eroded. However, given that no Silver trevally were otherwise identified in the samples it seems likely that these scutes were the remains of Jack mackerel. The six remaining fish species were of minor numerical importance, and together they constituted just 13% of the fish identified. These species were each represented by between one and three individuals.

Table 6.8: Pooled percent numerical abundance and percent frequency of occurrence (FOO%) for the identified species in the fresh food samples from Shy albatross chicks at Albatross Island, Tasmania, 1996/97 and 1997/98. Figures include only fresh prey items. Detailed composition for each sampling period is given in Appendix 6B. **Indicates deepwater species that may have been taken as trawler discards/by-catch.

	Number	% of prey class	% of total diet	FOO (%)
Fish				
Carangidae				
Jack mackerel (*Trachurus declivis)*	57	64.0	3.8	54.3
Mackerel or trevally (Carangid spp.)	4	7.0	0.3	3.7
Emmelichthyidae				
Redbait (*Emmelichthys nitidus*)	14	15.7	0.9	7.4
Moridae				
Red cod (*Pseudophycis bachus*)	3	3.4	0.2	3.7
Macrouridae				
Southern whiptail** (*Coelorinchus australis*)	1	1.1	<0.1	1.2
Gempylidae				
Barracouta (*Thyrsites atun*)	3	3.4	0.2	3.7
Apogonidae				
Big-eyed cardinalfish ** (*Epiogonus lenimen*)	1	1.1	<0.1	1.2
Latridae				
Trumpeter spp.	2	2.2	0.1	2.5
Serranidae				
Perch spp.**	2	2.2	0.1	2.5
Unidentified species	3	3.4	0.2	3.7
Squid				
Ommastrephidae				
Gould's squid (*Nototodarus gouldi*)	21	84.0	1.4	17.3
Sepiidae				
Cuttlefish *Sepia apama*	3	12.0	0.2	3.7
Argonautidae				
Argonaut *Argonauta nodosa*	1	4.0	<0.1	1.2
Unidentified species	0	0.0	0.0	0.0
Crustaceans				
Euphausiacea				
Australian krill (*Nyctiphanes australis*)	966	99.2	64.7	13.6
Isopoda	7	0.7	0.5	3.7
Unidentified species	0	0.0	0.0	0.0
Tunicates				
Pyrosomatidae				
Salps (*Pyrosomas spp.*).	408	100	27.3	44.4

6.3.4.5.2 Whole stomachs & incidental regurgitations from Albatross Island

Fish occurred relatively infrequently in these samples (FOO=25%, Table 6.2). Of 188 fish counted, 88 (46.8%) were identified to species or Family level. Otoliths from one species could not be identified (0.5%), while diagnostic remains from other fish were either absent or too eroded to identify (53.2%). In terms of both frequency of occurrence and numbers, Jack mackerel and Redbait were again the two most important fish species consumed (Table 6.9), together accounting for 57% of the identified fish. Seven additional Families of fish were identified, and one of these, the Macrouridae (Whiptails), accounted for a further 15% of the identified fish. Fish from the remaining six Families were incidental and represented in the samples by just one or two individuals (Table 6.9).

While the main species and groups of fish identified from the fresh food and whole stomach samples were similar, their relative abundance differed between these sample types (Tables 6.7 and 6.9, and Figure 6.4). Jack mackerel dominated in the fresh samples, (accounting for 64% of the identified fish), while in the whole stomach samples a wider array of species contributed to this portion of the diet (Figure 6.4), with no one species being as numerically abundant.

6.3.4.5.3 Size of the fish consumed

All uneroded otoliths were measured, and using the equations in Appendix 6A, estimates were made of the sizes of the Jack mackerel, Redbait and Barracouta *Thyrsites atun* consumed (Table 6.10). Species specific equations were used, and as size estimates for all species lay within the size range of fish used to develop the equations, size accuracy was assumed to be high.

The albatrosses generally consumed large fish, Jack mackerel which averaged 30 cm (366 g), Redbait of 17 cm (71 g) and Barracouta which averaged 64 cm in fork length and weighed 1.2 kg (Table 6.10). Most of the Jack mackerel consumed were mature individuals (mean length at maturity 27 cm, Figure 6.5, Webb 1976). The length frequency distribution of Redbait (Figure 6.5), however, indicated mostly subadult fish, as Redbait mature at a mean fork length of 21 cm (Kailola et al. 1993).

The size of Jack mackerel estimated from fresh food and opportunistic samples was similar (Fork length, $F_{1,36}$=0.21, p=0.650; Mass $F_{1,36}$=0.00, p=0.995), and data were

Table 6.9: Pooled percent numerical abundance and percent frequency of occurrence (FOO%) for the identified species in the whole stomachs and incidental regurgitations collected from Shy albatrosses at Albatross Island, Tasmania, 1994/95 to 1997/98. Detailed composition for each sampling period is given in Appendix 6C. ** Indicates deepwater species that may have been taken as trawler discards/by-catch.

	Number	% of prey class	% of total diet	FOO (%)
Fish				
Carangidae				
Jack mackerel (*Trachurus declivis*)	24	27.3	0.3	3.8
Mackerel or trevally (Carangid spp.)	8	89.1	<0.1	1.4
Emmelichthyidae				
Redbait (*Emmelichthys nitidus*)	26	29.5	0.3	1.7
Moridae				
Red cod (*Pseudophycis bachus*)	11	12.5	0.1	1.9
Macrouridae				
Whiptail spp.**	13	14.8	0.2	1.7
Berycidae**	1	1.1	<0.1	0.2
Clupeidae	1	1.1	<0.1	0.2
Merlucciidae	1	1.1	<0.1	0.2
Mugilidae (Mullet spp.)	1	1.1	<0.1	0.2
Platycephalidae (Flathead spp.)	1	1.1	<0.1	0.2
Trachichthyidae **	1	1.1	<0.1	0.2
Unidentified species	1	1.1	<0.1	0.2
Squid				
Ommastrephidae				
Gould's squid (*Nototodarus gouldi*)	1134	65.8	13.3	69.6
Sepiidae (Cuttlefishes)				
Sepia apama	169	9.8	2.0	23.5
Sepia novaehollandiae	297	17.2	3.5	31.4
Sepia spp.	23	1.3	0.3	3.9
Octopoteuthidae				
Octopoteuthis spp.	25	1.5	0.3	4.3
Onychoteuthidae				
*Moroteuthis ingens***	11	0.6	0.1	1.7
Cranchiidae				
Teuthowenia cf megalops	7	0.4	<0.1	0.9
Teuthowenia pellucida	1	<0.1	<0.1	0.2
Histioteuthidae				
Histioteuthis B4	3	0.1	<0.1	0.3
Histioteuthis ?celetaria	1	<0.1	<0.1	0.2
Octopodidae				
*Octopus australis***	10	0.6	0.1	1.7
*Octopus spp.***	14	0.8	0.2	1.7
Argonautidae				
Argonaut *Argonauta nodosa*	26	1.5	0.3	4.3
Cycloteuthidae				
Cycloteuthis sirventi	1	<0.1	<0.1	0.2
Enoploteuthidae				
Ancistrocheirus lesueri	1	<0.1	<0.1	0.2
Mastigoteuthidae				
Mastigoteuthis spp.	1	<0.1	<0.1	0.2
Unidentified cephalopods	11	0.6	0.1	1.4
Crustaceans				
Cirripedia				
Barnacle spp. (*Lepadomorpha*)	1	0.4	<0.1	0.2
Euphausiacea				
Australian krill (*Nyctiphanes australis*)	224	92.6	2.6	1.4
Isopoda	12	5.4	0.1	1.7
Decapoda				
Unidentified decapod crustacean	5	2.1	<0.1	0.9
Unknown species	1	0.4	<0.1	0.2
Tunicates				
Pyrosomatidae				
Pyrosomas spp.	6492	100	76.0	51.5

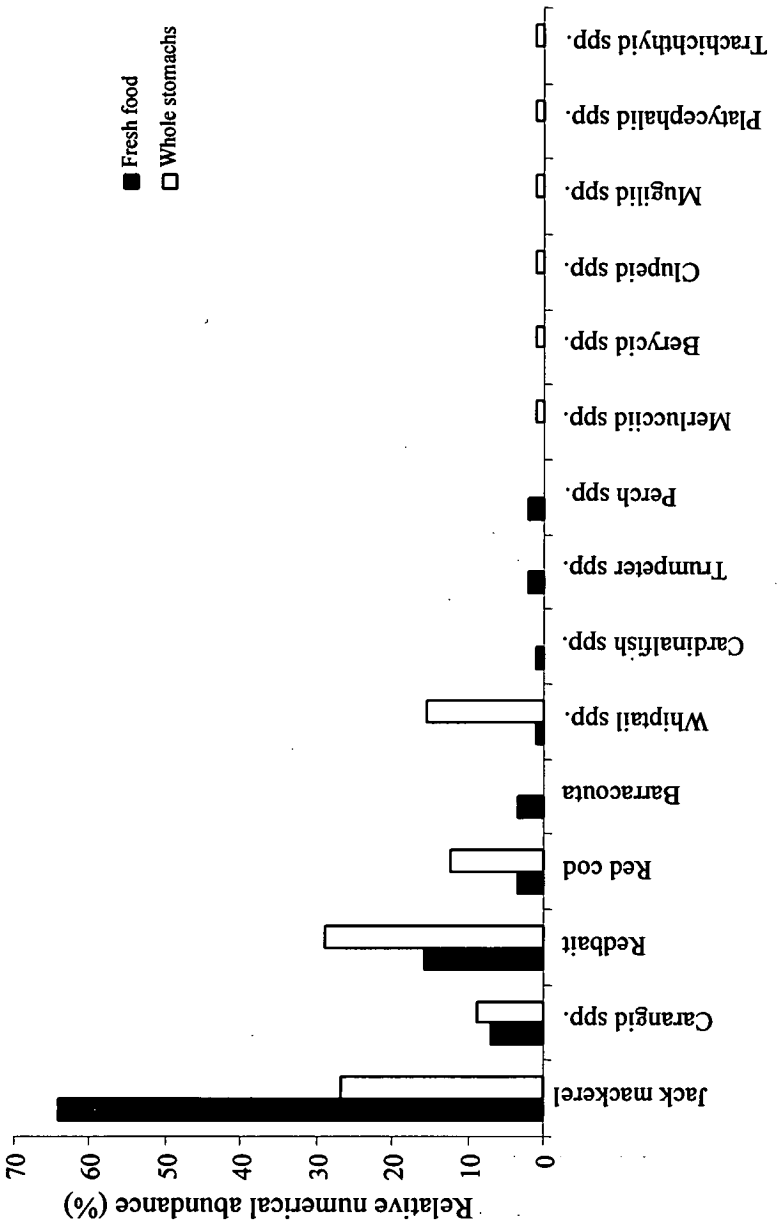


Figure 6.4: Relative numerical abundance of the fish species or groups occurring in the fresh and opportunistically collected diet samples at Albatross Island.

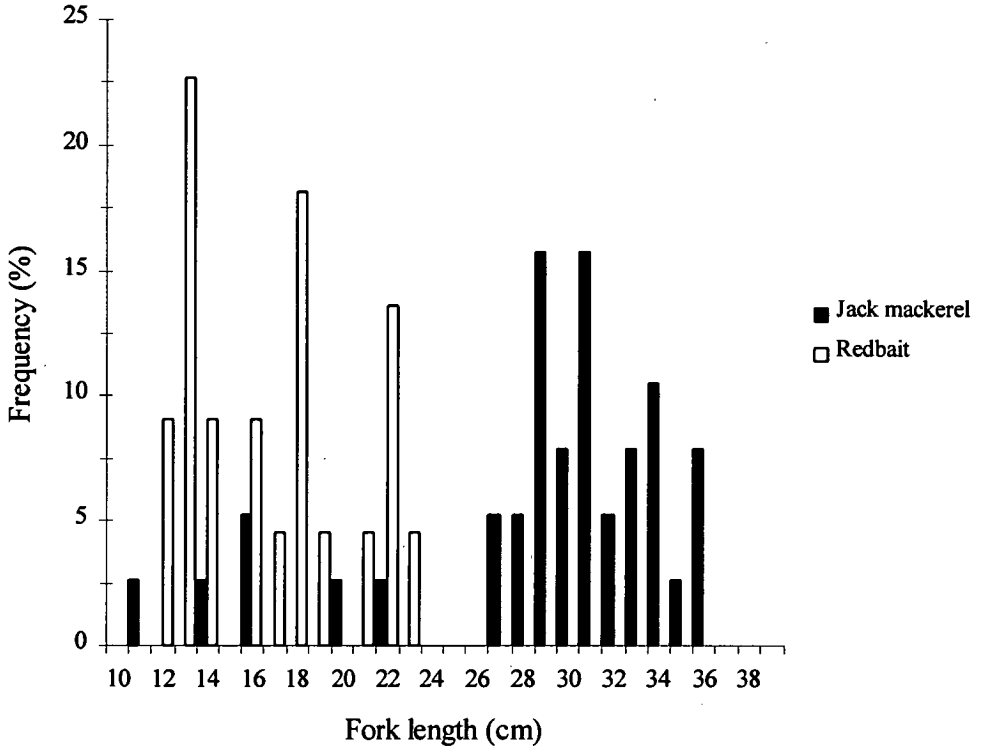


Figure 6.5: Frequency distributions of the estimated fork lengths of Jack mackerel (n=38) and Redbait (n=22) recovered from Shy albatross diet samples.

therefore pooled across sample types to assess size differences through time. There were differences between years in both the fork lengths and masses of the Jack mackerel consumed (two-way ANOVAs; $F_{2,31}$=8.30, p=0.001, and $F_{2,31}$=4.44, p=0.020), with fish being smaller in 1996/97 than in 1997/98 (26 ± 8.1 cm vs 32 ± 3.3 cm, and 278 ± 205.4 g vs 438 ± 133.9 g, respectively, Figure 6.6). There was, however, no intra-annual change in the size of the fish eaten, with both the fork lengths and masses of Jack mackerel being similar between mid- and late chick-rearing (two-way ANOVAs; fork length, 29 ± 7.5 cm vs 30 ± 3.9 cm, $F_{1,31}$=1.59, p=0.217, mass, 374 ± 207.4 g vs 357 ± 130.0 g, $F_{1,31}$=0.26, p=0.615, respectively).

Table 6.10: Estimated size of the fish consumed by Shy albatrosses during this study.

Species	n	Otolith length (mm) Mean ± SD (range)	Fork length (cm) Mean ± SD (range)		Mass (g) Mean ± SD (range)
Jack mackerel	38	8.9 ± 1.57 (4.3-10.7)	FL	29.5 ± 6.06 (11.8-36.6)	365.9 ± 173.72 (18.2-667.0)
Redbait	22	5.8 ± 1.01 (4.6-7.7)	FL	17.3 ± 3.59 (12.9-24.0)	70.6 ± 49.90 (22.0-187.3)
Barracouta	3	10.7 ± 0.69 (9.9-11.1)	FL	63.9 ± 5.83 (57.2-67.3)	1166.8 ± 307.03 (812.3-1344.1)

The limited number of measurable Redbait (n=22) precluded meaningful comparisons of fish size between breeding stages or years. For example, while there appeared to be an annual difference in the size of Redbait consumed ($F_{2,19}$=4.01, p=0.035), with fish from 1995/96 (15 ± 3.5 cm) being smaller than those from 1996/97 (19 ± 3.1 cm, Tukey's HSD, $p < 0.05$), 60% (6 of 10) of the 1995/96 fish originated from a single sample. As schools tend to be composed of similar sized fish, this apparent difference could have resulted from a single albatross exploiting a school of small Redbait rather than a real annual difference in the size of the fish available.

6.3.4.6 *Cephalopods*

6.3.4.6.1 Fresh food samples

In terms of frequency of occurrence, percentage by number and wet mass (Tables 6.2 and 6.5), cephalopods were less important in the fresh food samples than fish. Of 41 squid

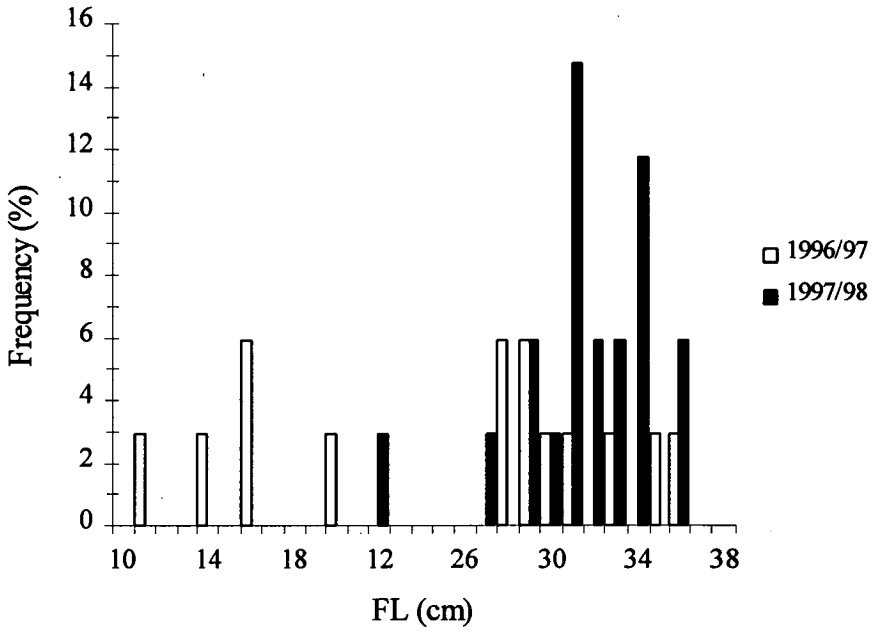


Figure 6.6: Frequency distribution of the estimated fork length of Jack mackerel recovered from Shy albatross diet samples in 1996/97 (n=14) and 1997/98 (n=20).

counted, 25 (61.0%) were identified to species level, and being represented by flesh only, the other 16 squid (39.0%) could not be identified. The three species present in the fresh food samples were Gould's squid, *Nototodarus gouldi*, a cuttlefish *Sepia apama*, and an argonaut *Argonauta nodosa*. Gould's squid accounted for 84% of the identified squid (Table 6.8) and this species was an important component of this portion of the diet during each period (Appendix 6B). Three cuttlefish were present (one in April 1997 and two in April 1998), accounting for 12% of the identified squid, while just one argonaut was found in February 1997. With the exception of February 1998, cephalopods contributed less than 10% by wet mass to the fresh portions of these samples (Table 6.5, Figure 6.1c).

6.3.4.6.2 Whole stomach samples

Overall, cephalopods dominated the whole stomach samples in terms of frequency of occurrence (Table 6.2), and in most periods they also dominated by number (Figure 6.2). Cephalopod presence was evident, almost without exception, from loose beaks and as they were often in a highly eroded state, some of these beaks had almost certainly accumulated through time. Notwithstanding, all identified squid were used to describe the species composition of this component of the diet.

Of 3,697 cephalopods counted, 1,724 (46.6%) were identified to species, Genus or Family level (Table 6.9, Appendix 6C), while 11 (0.3%) of the beaks could not be identified. These unidentifiable beaks were all from small squids, and diagnostic features of the beaks were lacking (N. Klages, pers. comm.). The remaining 1,962 beaks (53.1%) were too eroded to identify. Twelve squid species were identified from the samples, and a further four squid prey were identified to Genus/Family level (Table 6.9). Gould's squid was again the most commonly occurring cephalopod species (overall FOO=69.6%), and this species accounted for 65.8% of all beaks identified. Gould's squid was consistently the most important cephalopod species consumed, accounting for at least half of the beaks identified in each period (Figure 6.7).

The second most abundant squid was *Sepia novaehollandiae* a small cuttlefish. This species occurred in 31.4% of the samples and accounted for 17.2% of the beaks identified (Table 6.9). The occurrence of this species was not constant through time, however, and in both 1996 and 1998 it became relatively more abundant during the summer (from brood December/January to fledging in April, Figure 6.7 and Appendix 6C). The large cuttlefish *Sepia apama* also occurred frequently, in 23.5% of the samples, although it

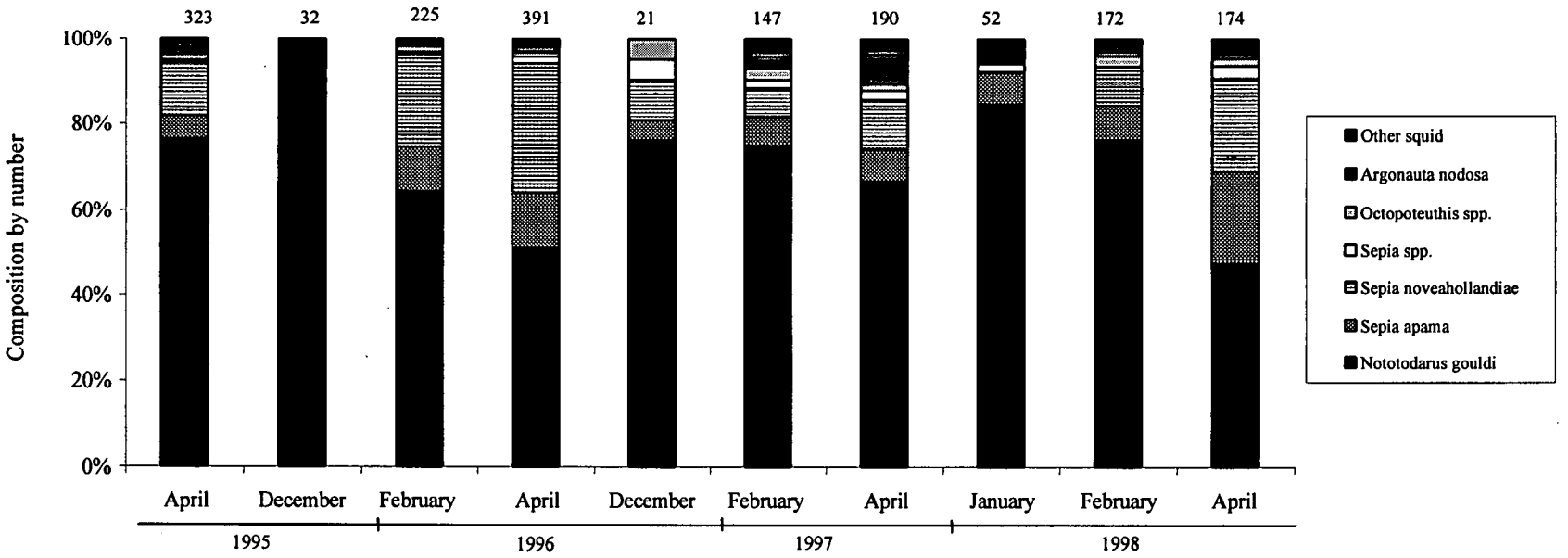


Figure 6.7: Contribution by number of squid species present in the opportunistically collected diet samples from Albatross Island. Squid species were included where they constituted ≥ 5% of the number of squid consumed in any one period.

accounted for just 9.8% of the beaks identified. Just three further cephalopod species, *Octopoteuthis spp.*, the argonaut *Argonauta nodosa*, and an unidentified small cuttlefish *Sepia spp.* occurred in more than 2% of these samples, together accounting for 4.3% of the identified beaks. The remaining nine species or types of squid occurred incidentally, and were each represented by just a few individuals. Together these nine groups accounted for just 3% of the identified beaks.

6.3.4.6.3 Size of the squid consumed

Only for Gould's squid were there sufficient numbers of measurable beaks to test for differences in squid size between sample types; as just one measurable *Sepia apama* and one measurable *Argonauta nodosa* beak were found in the fresh samples. The sizes of Gould's squid recovered from the fresh and opportunistic samples were similar during all periods (February 1997; t=-0.17, df=43, p=0.863, April 1997; t=0.884, df=79, p=0.380, February 1998; t=-0.096, df=97, p=0.924). Sample sizes were insufficient during April 1998 to test for size differences between sample types. However, as no size differences were apparent, beaks were pooled across sample types to assess differences between the breeding stages and years.

Of the 1,752 squid identified, beak measures and size estimates could be made for 1,170 (66.8%; Table 6.11) using the regression equations listed in Appendix 6A. Whenever possible species-specific equations were used, otherwise equations were taken from closely related taxa, with size estimates for all but two of the squid prey types (Histioteuthidae) derived from samples within the same Genus. Clearly substantial errors can result from application of Generic or Family level equations, but errors can also result from application of species-specific equations if the size range of prey falls outside the range of specimens used to derive the equation. Most conversion equations were adopted from Clarke (1986) and, unfortunately, the size ranges of specimens used to develop the equations were not stated. As a result, along with the size estimates an evaluation of equation reliability is given for each prey type (Table 6.11).

Histograms of the dorsal mantle length of squids with more than 10 measurable samples are shown in Figure 6.8. The dorsal mantle length of most squids consumed averaged greater than 100 mm (Table 6.11), while the most frequently consumed species ranged from an average of 115 mm for the small cuttlefish to 255 mm for Gould's squid. While the estimated dorsal mantle lengths accorded well with known size ranges for most species, masses of the Sepiids were somewhat suspect (largest *Sepia apama* in this study

Table 6.11: Estimated sizes of the squid eaten by Shy albatrosses. See Appendix A for regression equations and source references. LRL is lower rostral length (mm), HL is hood length (mm), and CR is crest length (mm). All measures are given as the mean± SD with the range of values indicated in parentheses. Equation reliability; 1, High, size calculated from equations derived from the same species, within the size range found in this study; 2, Moderate, sizes calculated from the same species, but outside the size range, or no size range stated; 3, Fair, size calculated from a different species within the same genus; 4, Poor, size calculated from a different genus within the same family.

Species	Measure	N	Beak size (mm)	Calculated mantle length (mm)	Calculated mass (g)	Equation reliability
Nototodarus gouldi	LRL	706	6.0 ± 2.03 (0.8 - 10.0)	255 ± 77.1 (57 - 407)	602 ± 442.3 (5 - 1997)	1
Sepia apama	HL	112	11.2 ± 1.97 (6.4 - 16.2)	243 ± 43.0 (138 - 352)	2698 ± 1846.2 (232 - 10068)	3
Sepia novaehollandiae	HL	270	5.3 ± 1.07 (2.0 - 8.6)	115 ± 23.5 (42 - 186)	140 ± 112.9 (2 - 770)	3
Sepia spp.	HL	19	4.4 ± 2.03 (1.6 - 8.4)	94 ± 44.3 (33 - 182)	126 ± 187.2 (1 - 700)	3
Octopoteuthis spp.	LRL	23	12.1 ± 2.67 (6.4 - 18.5)	209 ± 46.3 (111 - 320)	398 ± 194.9 (86 - 998)	3
Moroteuthis ingens	LRL	7	11.8 ± 0.97 (10.5 - 13.0)	454 ± 38.4 (402 - 501)	2551 ± 519.4 (1877 - 3223)	1
Octopus australis	CL	7	3.5 ± 0.97 (2.6 - 4.9)	92 ± 24.2 (70 - 127)	326 ± 274.5 (112 - 762)	3
Argonauta nodosa	CL	13	13.4 ± 5.61 (3.4 - 19.5)	88 ± 40.3 (17 - 132)	180 ± 124.6 (2 - 379)	1
Teuthowenia cf megalops	LRL	5	5.4 ± 1.22 (4.0 - 7.3)	233 ± 49.6 (175 - 310)	117 ± 63.1 (54 - 220)	3
Teuthowenia pellucida	LRL	1	4.5	196	71	3
Histioteuthis B4	LRL	3	5.7 ± 0.80 (4.9 - 6.5)	114 ± 17.81 (95 - 131)	284 ± 89.1 (194 - 372)	4
Histioteuthis ? celetaria	LRL	1	5.1	100	212	4
Cycloteuthis sirventi	LRL	1	11.4	353	762	2
Ancistrocheirus lesueri	LRL	1	7.5	264	1074	2
Mastigoteuthis spp.	LRL	1	6.8	196	300	3

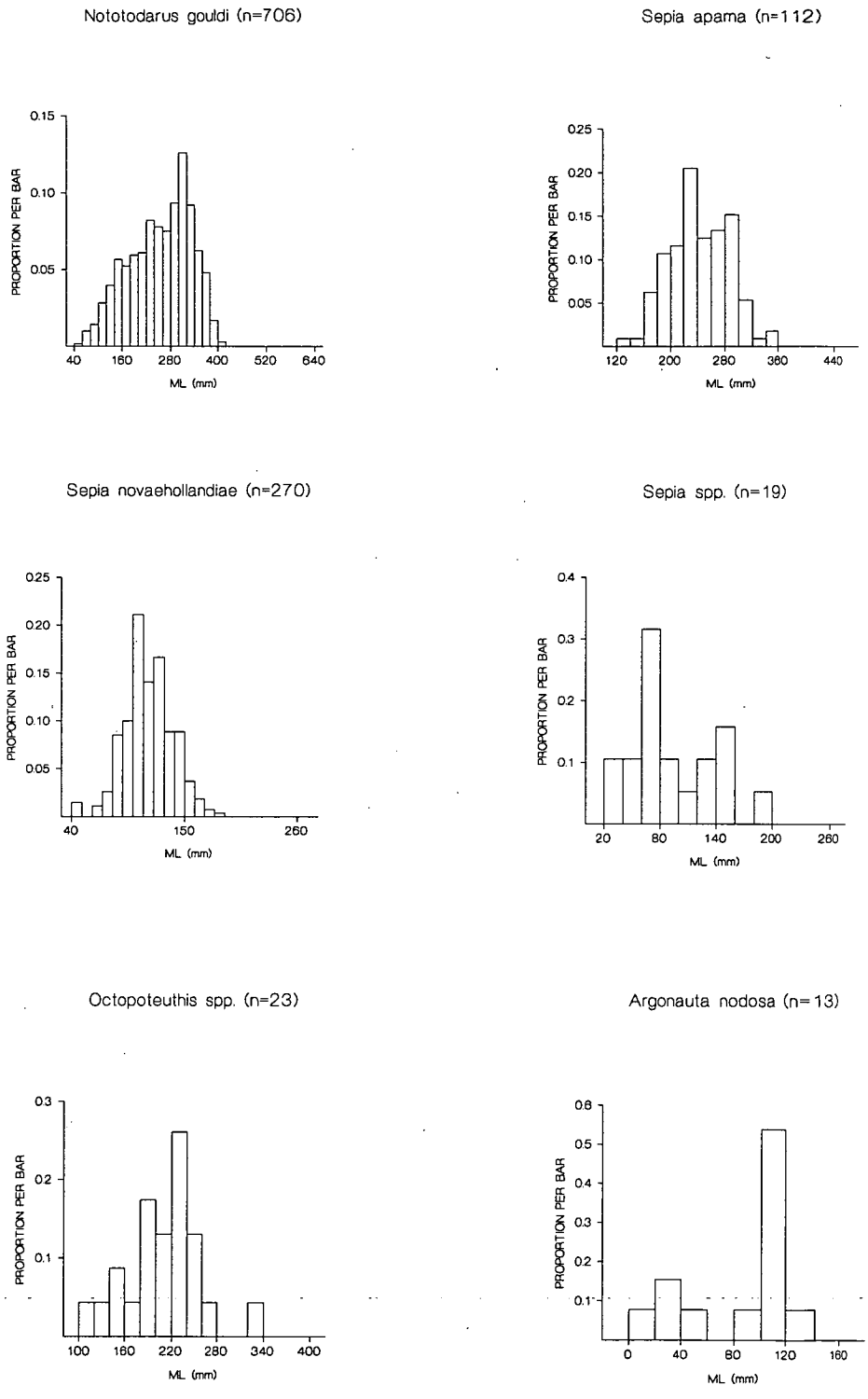


Figure 6.8: Frequency distribution of the calculated dorsal mantle lengths of the most numerous cephalopod species eaten by Shy albatrosses.

estimated to be 10.1 kg) given that the largest known individual weighed 6.2 kg (C.C. Lu cited in Gales et al. 1993). Certainly for this Family, then, mantle length would be the most accurate estimate of size.

While the overall frequency distribution of the dorsal mantle length of Gould's squid was unimodal (Figure 6.8), the sizes of the squids consumed were not constant through time (Figure 6.9). Squid size increased progressively throughout the rearing period (two-way ANOVA, $F_{2,536}$=103.2, $p < 0.001$, Figure 6.9), from chick-brood (December/January), when the squid averaged 165 ± 53.4 mm in length, to 287 ± 61.6 mm at fledging in April. This change presumably reflected squid growth. While there was no significant difference in the size of the squid consumed between years ($F_{2,536}$=2.77, p=0.0636, 1995/96 268 ± 71.5 mm, 1996/97 234 ± 83.0 mm, and 220 ± 83.4 mm), there was a significant interaction between breeding stage and year ($F_{4,536}$=7.57, $p < 0.001$, Figure 6.10). Despite the squid consumed in December 1995/January 1996 being somewhat smaller than those consumed during the same period in the other two years, squid eaten in February and April 1996 were larger than average (Figure 6.10).

Cuttlefishes were consumed in significant quantities between mid-chick rearing and fledging (Figure 6.7), and the sizes of these prey were constant between years (two-way ANOVAs, *Sepia apama*, $F_{2,94}$=2.65, p=0.076, *Sepia novaehollandiae* $F_{1,223}$=1.66, p=0.192) and between stages of the breeding season (two-way ANOVAs, *Sepia apama*, $F_{1,94}$=1.93, p=0.169, *Sepia novaehollandiae* $F_{1,223}$=1.81, p=0.180).

6.3.4.7 *Crustaceans*

6.3.4.7.1 Fresh food samples

Crustaceans occurred in 17% of the fresh food samples, and while they accounted for a significant number of the overall prey items identified (64.7%), they contributed a negligible amount to sample wet mass (0.0-8.4%, Table 6.5). Just two crustaceans were present in the fresh food samples; Australian krill *Nyctiphanes australis* which accounted for 99.2% of the 974 crustaceans, and seven isopods (of unidentified species) which accounted for the remaining 0.7% of the items from this prey class.

Consistent with patterns of occurrence for crustaceans overall, the occurrence of krill varied substantially through time, occurring frequently and accounting for a substantial number of the identified prey items only during February 1997 (Figure 6.1). While krill

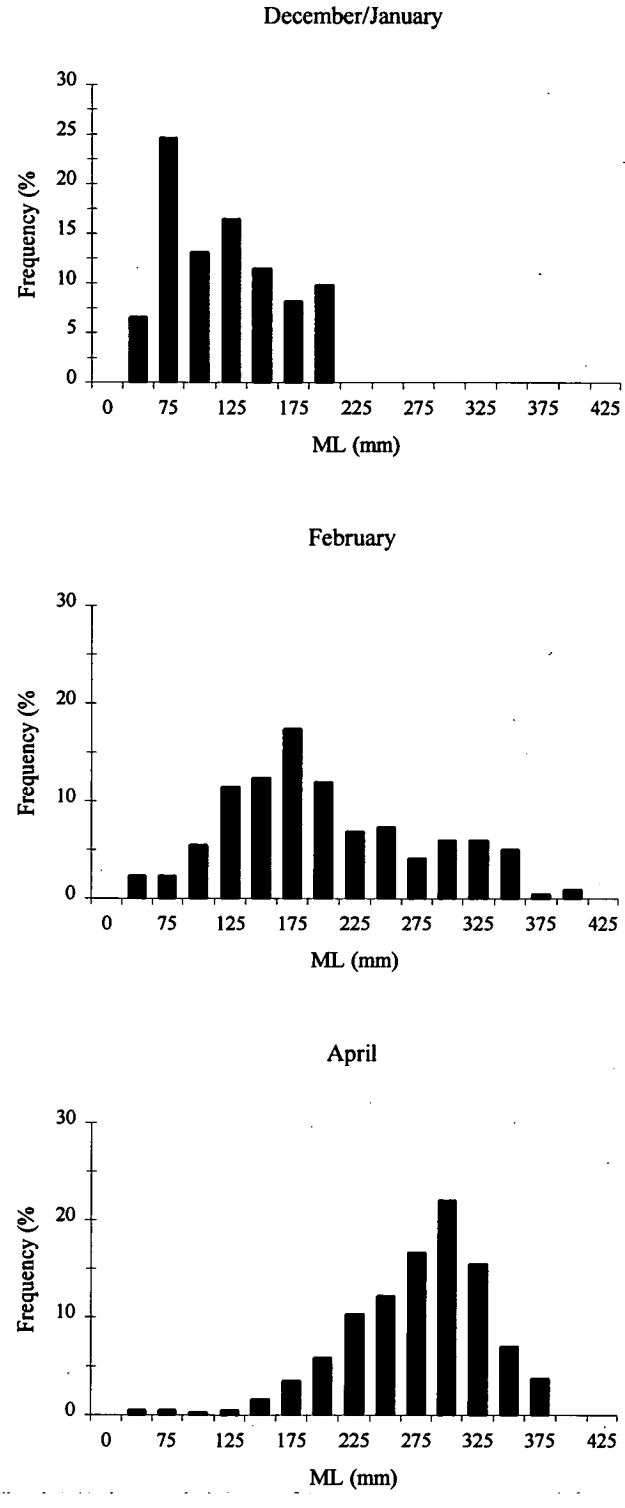


Figure 6.9: Frequency distribution of the calculated mantle lengths (ML) of Gould's squid consumed by Shy albatrosses from brooding (December/January) to fledging (April) across the study years.

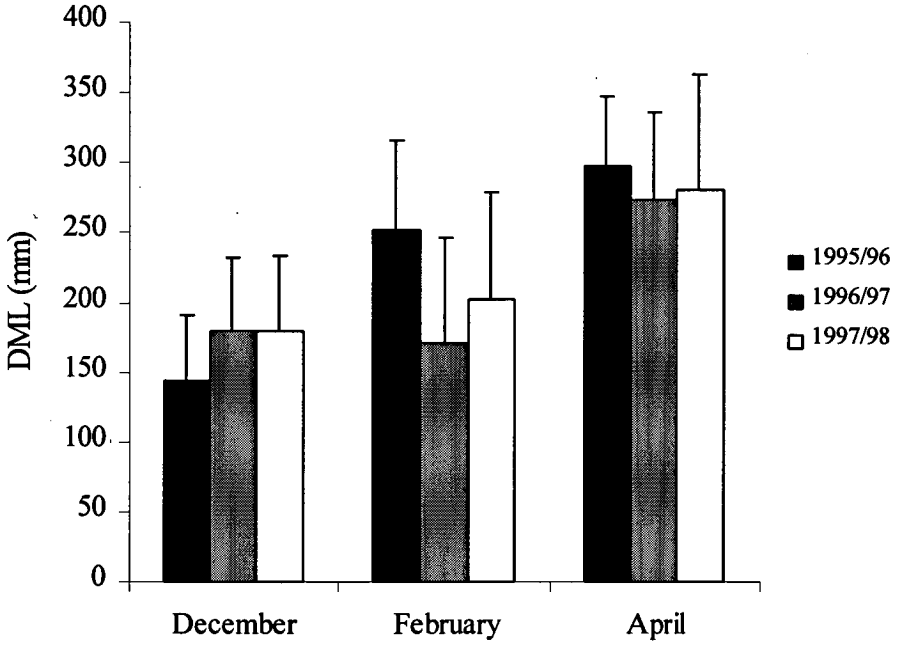


Figure 6.10: Mean (± 1 SD) mantle length of the Gould's squid eaten by Shy albatrosses during each sampling period and year.

consumption appeared secondary in many instances (being present in the stomachs of partly digested fish and squid), in one sample in particular, the krill remains were fresh and they contributed 100% to the solid portion of the meal. Isopods occurred infrequently, and at least a portion of them were thought to parasitize fish, and were possibly secondarily ingested.

6.3.4.7.2 Whole stomach samples

Crustaceans also occurred infrequently in these samples (FOO=6%) and they accounted for just 3% of all prey items (Table 6.2). However, a wider variety of crustaceans were present in whole stomach as opposed to fresh food samples, with representatives of four crustacean species or groups. In terms of numbers, however, krill was again dominant (92.6% of the identified crustaceans, Table 6.9). Isopods were present in less than 2% of the samples, and they accounted for 5% by number of the crustaceans in the diet. One crustacean was unidentifiable. While the origin of the remaining crustaceans, which includes the Barnacle *Lepadomorpha* (Tables 6.8 & 6.9) and shell fragments from a variety of unidentified decapod crustaceans, is unknown, it seems possible that they could have been fish prey that were secondarily ingested.

6.3.4.8 *Tunicates*

In both the fresh food and whole stomach samples, salps *Pyrosomas spp.* occurred frequently (44.0% and 51.5%, respectively) and accounted for a substantial number of the identified prey items (27.3% and 76.0%, respectively, Tables 6.7 and 6.9). Variability in either the distribution or abundance of salps might be expected between years, as they occurred much more frequently in the samples collected during 1996 and 1998 than at any other time (Figures 6.1 & 6.2, Appendices 6B & 6C). Overall FOO for salps in the stomach samples was greater than 50% in February and April 1996, as well as throughout 1998 (Figure 6.2). In these periods salps also accounted for more than 50% of the identified prey. Trends for the fresh food samples were similar, with salps occurring more frequently in 1998 than in 1997, and dominating in terms of numbers in 1998. As many as 77 salps were recovered from single fresh food samples, while a maximum of 918 salps was recovered from a single whole stomach.

While salps occurred frequently, and often in large numbers, they never contributed substantially to sample wet mass (Figure 6.1c and Table 6.5). The value of 10% in April 1998 was strongly influenced by two samples whose solid mass (just 0.4g and 8.9g)

consisted only of salps. Both of these samples were small (75g), and contained mainly liquid.

6.3.5 *Incidence of trawler by-catch in the food delivered to chicks*

Deep water and benthic inhabitants, such as those indicated by asterisks in Tables 6.7-6.9, seem unlikely to be naturally obtainable by albatrosses. Fish such as the Whiptails, Cardinalfishes (*Epigonus lenimen*), Sawbellies (Trachichthyids), Perch (Serranids), and Alfonsins/Snappers (Berycids) are all deep water species that frequently occur as by-catch in the trawl fisheries off Tasmania's west coast (Last et al. 1983). Their occurrence in albatross food samples likely reflects that they were scavenged. Of the identified fish, 16 of 90 (18%) from the whole stomachs and incidental samples (Albatross Island and Pedra Branca pooled) and 4 of 87 (5%) from the fresh food samples were likely to have been scavenged.

While the situation for squid is less obvious, being benthic inhabitants and known "sinkers" after death (Lipinski & Jackson 1989), both *Moroteuthis ingens* and the Octopods could have potentially been taken as fisheries waste. Adding these species to squids for which floating/sinking status is unknown (Argonauts, Cycloteuthids, Enoploteuthids, Lipinski & Jackson 1989, Croxall & Prince 1994), indicates that species potentially scavenged from fishing operations constituted 3.7% of the identified squid (65 of 1,752).

6.4 DISCUSSION

In a recent review, Cherel & Klages (1998) provided a detailed synthesis of the foods consumed by albatrosses, and outlined both the main collection methods and the biases inherent to each. Albatross food samples have originated from 1) the stomachs of birds killed at-sea, 2) fresh samples of food regurgitated by adults or chicks, and 3) from the collection of casts previously regurgitated by adults or chicks on the nesting grounds (Cherel & Klages 1998). As each sampling regime has it's own set of associated biases, both the type of samples collected and the choice of methods for analyzing them, can greatly influence interpretation of the diet composition.

Variable residency times and differential digestion of diagnostic prey remains in the gut are the two main sources of bias encountered when interpreting dietary data from marine predators. Both biases were evident in this study, and they could likely account for differences in composition of the two main sample types. Composed mainly of

indigestible chitin, cephalopod beaks can persist in the stomachs of seabirds for periods exceeding 50 days (Furness et al. 1984). Cephalopods dominated the composition of the whole stomach samples, both in terms of frequency of occurrence and number during all sampling periods. Being instead composed mainly of calcium carbonate, the remains of fish prey are readily digested or voided from predator stomachs (Gales 1988). Fish prey dominated the fresh food samples in terms of frequency of occurrence and percent by mass, throughout the study.

Depending then upon the actual composition of the diet and the type of samples collected, there is potential for cephalopod importance to be overestimated and conversely the importance of prey classes which digest rapidly, such as fish or invertebrates, to be underestimated. This is, of course, a broad generalization, as even within a single prey class there would be selective bias against, for example, small squid beaks that may be completely digested or voided, and bias towards fish with large or robust otoliths. Unfortunately, however, no method of diet collection or analysis is completely free from bias, and results of such studies must be carefully interpreted in light of the methods used.

In this study, the fresh food samples likely provided the most reliable estimate of the diet composition. Biases resulting from the accumulation of prey (both fish and squid) were minimized by limiting analyses to the fresh portion of the diet (prey items with attached flesh). However, as birds were simply inverted (and not stomach flushed) to obtain the samples, they would have likely included only partial contents of the proventriculus. While most of the food was thought to be ejected, there was no way of quantifying either the amount of food remaining in the stomach or the potential bias of partial sampling. Also, despite the relatively large number of fresh samples collected (n=96), sampling was confined to just two months of the seven month breeding cycle, and likely adequately reflected the diet composition only during the period of chick care.

Despite being mainly fish eaters, the rapid digestion of fish, and the tendency for squid beaks to accumulate through time resulted in the latter prey type predominating samples taken from dead chicks. Judging from the highly eroded state of some of the squid beaks, it seemed likely that they had been accumulating in the stomachs since hatching. Notwithstanding, dissections ensured that the contents of both the proventriculus and the ventriculus (ie, all prey remains) were obtained. The large number of samples collected, the temporally extended sampling regime, and concurrent collection of fresh food samples, allowed both detailed assessments of the squid component of the diet and proper interpretation of its relative importance.

6.4.1 *Comparison with other albatross species*

6.4.1.1 *Meal sizes and solid and liquid constituents*

Shy albatross chicks receive relatively small meals (371 ± 166.6 g, range 40-840 g) every 22 ± 17.7 hrs (Chapter 7). During some periods the mass of the fresh food samples (approximately 400 g in April and just over 500 g in February, range 35-1,085 g) was significantly larger than the mass of single meals delivered to chicks. The implication was that at certain stages of the breeding season, particularly when the chicks were young and being provisioned at a high rate, that food samples thus collected were likely to contain contents of more than the single meal. While this was previously noted for Wandering albatrosses (Cooper et al. 1993), the magnitude of the difference would likely be greatest for species with higher feeding frequencies. Prince (1980) noted that fresh food samples collected from adults were actually smaller than the size of single meals feed to chicks, indicating that when samples were collected in this manner, the bias was likely to be in the opposite direction.

Fresh food samples contain both solid and liquid fractions, and the liquid fraction generally ranges between 50 and 80% of sample mass (Cherel & Klages 1998 and references therein). Samples collected from Shy albatross chicks were similar and contained, on average, 44% liquid and 56% solid, by mass. However, as appears to generally be the case, there was substantial variation in the proportion of liquid in the samples, ranging from 15-100% of sample mass. The quality of the liquid also varied considerably from almost pure water to a dense, deep orange oil. The quality and energy density of liquid fractions reportedly vary according to the type of prey consumed (Cherel & Klages 1998 and references therein).

6.4.1.2 *Prey class consistuents*

Synthesized by Cherel & Klages (1998), the relative importance of the different prey classes to the diets of albatrosses are reiterated here. In terms of percentage by mass, squid predominates the diets of Wandering, Royal, Laysan *Phoebastria immutabilis*, Grey-headed *Thalassarche chrysostoma*, Sooty *Phoebetria fusca* and Light-mantled sooty *Phoebetria palpebrata* albatrosses (Croxall et al. 1988, Imber 1991, Cooper et al. 1992, Ridoux 1994, Cooper & Klages 1995, Reid et al. 1996). Fish, alternatively, predominates in the diet of Shy, Black-footed *Phoebastria nigripes*, Yellow-nosed *Thalassarche chlororhynchos*, and Black-browed albatrosses *Thalassarche melanophris*, at least at some sites (Harrison et al. 1983, Weimerskirch et al. 1986, Croxall et al. 1988,

Ridoux 1994, Reid et al. 1996, Waugh & Weimerskirch 1998, this study). Caution must be used when interpreting these generalizations, though, as both the sample sizes and types differed between studies. There are also issues of spatial and temporal variation, and as concluded both by Croxall & Prince (1996a) and Cherel & Klages (1998), albatross diet composition is likely strongly influenced by the availability of accessible prey (≤ 10m depth) within the foraging zones.

There is considerable inter-annual variation in diet composition for Black-browed albatrosses at South Georgia (Prince 1980, Croxall et al. 1988, Reid et al. 1996); krill dominates in good years while there is a shift to fish in years of poor krill availability. With respect to spatial variation, the diets of both Black-footed and Laysan albatrosses were similar at two different breeding sites in the Hawaiian Islands (Harrison et al. 1983), while major dietary differences were noted for populations of Black-browed albatrosses breeding in the Falkland Islands (Thompson 1992). As different populations, age classes and sexes of albatrosses have since been shown to segregate their foraging zones at sea (Weimerskirch et al. 1988, Brothers et al. 1997, Weimerskirch et al. 1997b, Prince et al. 1998), consequent widespread spatial variation in the diet composition might not be surprising (see also Croxall & Prince 1996a).

Squids are important prey of albatrosses, particularly those from the Families Ommastrephidae and Onychoteuthidae (Croxall & Prince 1996a, Cherel & Klages 1998). Onychoteuthids are important to Wandering and Royal albatrosses, with birds taking adult squid that are most likely scavenged from the surface (Croxall & Prince 1994, Cherel & Klages 1998). Ommastrephids occur in albatross diets worldwide, being particularly important in the diets of smaller albatrosses in the Southern Ocean (Croxall & Prince 1996a, Cherel & Klages 1998). The specific Ommastrephid preyed upon varies according to local abundance; *Martialia hyadesi* is important to the diet of Black-browed and Grey-headed albatrosses at South Georgia, *Illex argentatus* is taken by albatrosses in the Falkland Islands (Rodhouse et al. 1993, Thompson 1992), and *Nototodarus gouldi* is important to Shy albatrosses in Australian waters. The bulk of the Ommastrephids taken by these species are juveniles (Croxall & Prince 1996a, Cherel & Klages 1998).

Epipelagic fish are common prey of albatrosses foraging at low latitudes in both the Northern (Harris 1973, Harrison et al. 1983), and Southern Hemispheres (Barton 1979, this study); with Jack mackerel and Redbait commonly consumed by Shy albatrosses in this study. Such fish are, however, uncommon at higher latitudes, and benthic species replace them, forming the bulk of the fish component of the diet for the sub-Antarctic

species (Cherel & Klages 1998). The predominance of deepwater species indicates scavenging from fishing operations (Reid et al. 1996), but, as some species are known to float after death, they may also be naturally available to albatrosses at the surface (Cherel unpubl. data, cited in Cherel & Klages 1998).

Salps were frequently encountered in Shy albatross food samples, but overall they contributed little to mass. Salps have also been reported in the diets of Wandering (up to 90 individuals in one sample, Imber 1992) Buller's *Thalassarche bulleri* (West & Imber 1986), Black-browed and Grey-headed albatrosses (Tickell 1964), and they had been previously recorded for Shy albatross at Albatross Island (Green 1974). Large aggregates were often found in samples in this study (up to 918 salps in one stomach), and as such it was thought to be the sexual, aggregate form consumed. Many of the salps found here were intact, and this is interesting given that they have only been previously recorded in a highly digested state. This difference may simply reflect the proximity of Shy albatross foraging grounds to the breeding colony (Brothers et al. 1998, Chapters 3 & 8), but it may also indicate that salps are at least somewhat resistant to digestion.

6.4.1.3 *Scavenging vs predation*

As squid predominates the diet of many albatross species, and squid are mainly deepwater inhabitants, there has long since been debate regarding the manner in which albatrosses catch their prey. That is, whether albatrosses are mainly scavengers or predators, and related to this, whether they feed mainly during the day or the night (Prince & Morgan 1987, Lipinski & Jackson 1989, Weimerskirch & Wilson 1992, Croxall & Prince 1994, Cherel & Klages 1998). Reviewing available evidence on the biology and behaviour of both squids (mainly size, buoyancy, bioluminescence, and diel vertical migrations), and albatrosses (foraging ranges, diving capacities, and timing of feeding), Croxall & Prince (1994) concluded that while Wandering and Light-mantled sooty albatrosses perhaps scavenged a significant proportion of their squid prey, Grey-headed and Black-browed albatrosses seemed unlikely to do so.

The characterization for Shy albatrosses seems less complicated. Adult Shy albatrosses forage exclusively over the southeast Australian continental shelf, and while they travel both during the day and night, much of their movement occurs during the day (Brothers et al. 1997, Chapters 3 & 8). During the period of chick care, Jack mackerel and Redbait, and to a lesser extent, Gould's squid dominate the diet. Both Jack mackerel and Redbait form surface schools over the southeast Australian continental shelf during summer and autumn, where they feed primarily upon Australian krill (Williams & Pullen 1993).

Schools form just after daylight and on cloudy days can persist in surface waters until dark (Williams & Pullen 1993). While adult Gould's squid are found most abundantly at 50-90 m (C.C. Lu unpubl. data, cited in Gales et al. 1993), they have also been observed taken by albatrosses at the surface during the day (Barton 1979). The majority of Gould's squid eaten by Shy albatrosses, however, were juveniles and juveniles of other Ommastrephid species are found in surface waters in other parts of the world (Croxall & Prince 1994, Cherel & Klages 1998). Shy albatrosses capture their food by making plunge and swimming dives to 8 m depth exclusively during daylight hours (Hedd et al. 1997, Chapter 4). Given that the main prey species are accessible in surface waters during the day, these features combine to indicate both that Shy albatrosses are largely predatory in their foraging behaviour, and that most, if not all of their prey can be accessed live from surface waters during the day.

6.4.1.4 *Prey size and the number of items per sample*

Albatrosses consume prey that vary widely in size, but there is a general correspondence between prey and predator size, with larger albatrosses generally consuming larger prey (Croxall & Prince 1994, Cherel & Klages 1998). Albatross prey ranges from less than 20 mm in length with weights less than 1 g (Australian krill taken by Shy albatrosses), to squids exceeding 1,000 mm in mantle length and weighing over 9,000 g (Wandering albatrosses, Cooper et al. 1992). Shy albatrosses also consumed variable sized prey; the largest fish taken was a Barracouta, estimated at 673 mm in fork length and 1,344 g, while the largest squid *Moroteuthis ingens* had an estimated mantle length of 501 mm. On average, the prey consumed by Shy albatrosses was relatively large; Jack mackerel averaged 295 ± 60.6 mm, Gould's squid averaged 255 ± 77.1 mm, and Redbait averaged 173 ± 49.9 mm in fork length. The largest Jack mackerel found in the samples (366 mm fork length, 667 g) perhaps approaches the upper size limit of prey the birds can handle whole (or live). Thompson & Riddy (1995) indicated that fish in excess of 400 mm were dismembered before being eaten by Black-browed albatrosses.

The number of prey items recovered in albatross food samples are often not reported, however, when reported, numbers are generally high; 15.7 ± 29.2 items (range 1-125) for Wandering albatross chicks at Marion Island (Cooper et al. 1992), and an average of 15 and 32 items per sample for Black-footed and Laysan albatrosses in the Hawaiian Islands (Harrison et al. 1983). Just 1.7 prey items were reported per sample for Wandering albatrosses at the Crozet Islands (Ridoux 1994), with birds generally consuming a small number of relatively large prey items (Cherel & Klages 1998). Care must be taken

interpreting these numbers, however, as they are not directly comparable. While accumulated squid beaks were excluded from averages for Wandering albatrosses, they were included in averages for the Hawaiian birds. 17.1 ± 81.55 items (range 1 - 773) were recovered in the fresh samples from Shy albatrosses in this study. While most fresh samples contained just one or two prey items, large numbers of small prey (eg, krill or salps) in some samples inflated the overall average. When considering just the fish and squid components of the diet (which in each period accounted for more than 90% of sample mass), samples contained just 1.9 ± 1.31 items.

6.4.2 *Comparison with an earlier study at Albatross Island*

The only other dietary study for this species comes from the analysis of 75 regurgitate samples collected from chicks at Albatross Island in January and February of 1973 (Green 1974). The mass of the samples collected and occurrence of the major prey classes in the previous and current studies are indicated in Table 6.12. Samples taken in both periods were similar in mass, ranging from less than 100 g to just over 1,000 g, and there were some similarities in occurrence for the major prey classes (Table 6.12).

The occurrence of salps was similar (FOO=40% and 32%), however, fish was relatively more common in this study (FOO=92% vs. 59%), while squid and crustaceans were relatively less common (FOO=51 vs. 33% and FOO=35 vs.14%, respectively, Table 6.12). The higher occurrence of squid in Green's study may indicate that accumulated beaks were included in the totals, or it could possibly represent a real change in the importance of squid between years. Differences, however, in the occurrence of crustaceans seemed real. Prawns *Gnathophausia spp.* occurred in 29% of the samples collected in 1973, while they were not detected in this study.

Table 6.12: Frequency of occurrence (%) and mass (g) of the fresh food samples collected from Shy albatross chicks at Albatross Island by Green (1974) and in this study (1995-1998).

	Frequency of occurrence (%)	
Prey class	Green (1974)	This study
number of samples	n=75	n=91
Fish	59	92
Cephalopods	51	33
Crustaceans	35	14
Tunicates	32	40
Sample mass (g)	80 - 1,050	50 - 1,085

Jack mackerel was noted as an important component of the fish portion of the diet in 1973; identified in 20% of the samples and accounting for 75% of the identified fish. None of the squid from Green's samples were identified, however, a whole squid collected incidentally in the colony was identified as Gould's squid. Given the available information, and considering the different proportions of the diet samples identified in the two studies, the composition of the diet seems to have been broadly similar through time.

6.4.3 *Biology of the prey and implications for spatial & temporal variation in diet composition*

At Albatross Island, there was little inter- or intra-annual variation in either the major prey classes, or in the species composition of the diet. Data provided by CSIRO (Hobart) also indicated little variation in oceanographic conditions (particularly sea surface temperatures, SST) in the foraging zone of this population either within or between years. However, given differences in the distribution and relative abundance of the main prey species north and south of Tasmania, spatial variation in Shy albatross diet composition might be expected.

Recent studies of the Australian fur seal *Arctocephalus pusillus doriferus*, for example, indicated spatial variation in the diet composition between the breeding colonies in Bass Strait and the haul-out sites off southern Tasmania (Gales et al. 1993, Gales & Pemberton 1994). Briefly, seals from Bass Strait consumed relatively more cephalopods (mainly Gould's squid) and relatively less Redbait than seals sampled off the south coast. These differences accord well with the distributions of prey, as the highest concentrations of Gould's squid are found in western Bass Strait (Winstanley et al. 1983), and Redbait are more locally abundant than Jack mackerel off the south coast (H. Williams unpubl. data, cited in Gales & Pemberton 1994). While the overall species composition of the diet for Shy albatrosses at Pedra Branca and Mewstone (off the south coast) would likely be similar to that described at Albatross Island in the north, the relative importance and occurrence of the species would likely vary with local abundance.

Given the more dynamic oceanographic conditions off the east coast of Tasmania, there is also potential for inter-annual variation in the availability of prey to birds breeding at the southern colonies, particularly Pedra Branca (Brothers et al. 1998, Chapters 3 & 8). Krill abundance, and the surface schools of Jack mackerel that form to feed on them, decrease when waters at the surface are warm (Williams & Pullen 1993, Young et al. 1993 & 1996). Presumably such changes in surfacing patterns would effect the availability of fish to predators such as albatrosses, which are restricted to feeding within 10 m of the

surface (Prince et al. 1994, Hedd et al. 1997, Huin & Prince 1997). While Jack mackerel is the main prey species delivered to chicks at Albatross Island, it's seasonal availability in surface waters (Williams & Pullen 1993), indicates that the birds must utilize alternative prey sources at other times of the year.

Gould's squid was the most important of the cephalopod species consumed. It is the most abundant cephalopod in the region, and is found predominantly over the shelf (C.C. Lu cited in Gales et al. 1993). While abundant throughout the study, the sizes of squids varied through time, becoming progressively larger from December through April, presumably reflecting growth. There was also inter-annual variation in the sizes of squids consumed, indicating either that the growth of Gould's squid in Bass Strait is not constant between years, or that the timing or duration of spawning differs between years (Smith 1983, Winstanley et al. 1983, Kailola et al. 1993).

6.4.4 *Comparison with other seabird and marine mammal species in the region*

Jack mackerel and Redbait are important dietary items for all the large marine homeothermic predators studied in the Tasmanian region to date (Shy albatrosses, Australasian gannets *Sula serrator*, Australian and New Zealand *Arctocephalus forsteri* fur seals) and depending on the locality from which samples were taken, the same holds true for Gould's squid (Brothers et al. 1993, Gales et al. 1993, Gales & Pemberton 1994, Lake 1997). The frequency of occurrence and sizes of prey consumed by albatrosses, gannets and fur seals are given in Table 6.13.

Jack mackerel occurred most frequently in the albatross diet, whereas Redbait was most prevalent in the diet of both the gannets and Australian fur seals off southern Tasmania. Jack mackerel and Redbait, however, were found in similar proportions for Australian fur seals in Bass Strait and New Zealand fur seals off the south coast of Tasmania. The Jack mackerel consumed by the albatrosses were larger than those eaten by gannets (by 12 cm), or Australian fur seals (by 8 cm), but similar in size to those eaten by New Zealand fur seals (Brothers et al. 1993, Gales & Pemberton 1994, Lake 1997). Similarity in the size of different prey types consumed by gannets suggests a ceiling on the size of prey that can be handled effectively (Brothers et al. 1993). Differences in the sizes of Jack mackerel consumed by albatrosses and Australian fur seals could reflect inter- or intra-annual variation in the size of fish available, vertical stratification of fish by size in the water column (Stevens et al. 1984), temporal, or geographic differences in the sampling locations. Interestingly, similar sized Redbait (16-17 cm fork lengths) were consumed by all the predators. Schools of Redbait tend to be composed of similar sized individuals,

suggesting perhaps that all predators exploit schools near the surface, and/or that Redbait of this size preferentially feed near the surface where they are more vulnerable to predation.

Table 6.13: Frequency of occurrence (FOO%) and size (FL in cm for fish, ML in mm for squid) of the Jack mackerel, Redbait and Gould's squid consumed by seabirds and marine mammals in the Tasmanian region. For Shy albatrosses FOO is stated for the fresh food samples only.

Species & site	n	Jack mackerel		Redbait		Gould's squid		Source
		FOO	Size	FOO	Size	FOO	Size	
Shy albatross (Albatross Is)	91	54.3	29.5 ± 6.1	7.4	17.3 ± 3.6	17.3	255 ± 77.1	this study
Gannet (Pedra Branca)	109	19.3	17.1 ± 4.9	71.6	16.7 ± 2.1	-	-	Brothers et al. (1993)
Australian fur seal (various)	340	12.6	21.2 ± 2.8	23.5	17.0 ± 1.2	12.6	239 ± 69.9	Gales et al. 1993; Gales & Pemberton 1994
New Zealand fur seal (Maatsuyker Is)	279	21	31 ± 5	22	16 ± 4	-	-	Lake (1997)

6.4.5 *Interactions with fisheries*

There are many types of interactions, both direct and indirect, between albatrosses and fisheries, but just two issues relating directly to the composition of the diet will be discussed here. The first is artificial provisioning, where species that are either not naturally available to albatrosses become so, or alternatively, naturally available prey become relatively more abundant through fisheries by-catch and discarding procedures. The second interaction is potentially competitive, where the same species are taken both by albatrosses and commercial fisheries.

In order to estimate the contribution of fisheries discards to the diet it is necessary to understand the vertical distribution of prey species within the water column. The major prey species of the albatrosses surface school to forage (Jack mackerel, Redbait and Gould's squid), or they migrate diurnally to surface waters (Gould's squid) and become naturally accessible to the albatrosses. Albatrosses, however, are enthusiastic followers of fishing boats where they scavenge baits, offal and discarded by-catch (Ryan & Moloney 1988, Thompson 1992, Thompson & Riddy 1995). There is a significant effort trawl fishery over the outer continental slope off western Bass Strait and the west coast of

Tasmania, and these areas lie within the foraging zones of birds from the Albatross Island population (Brothers et al. 1998, Chapters 3 & 8). Shy albatrosses are known to utilize the by-catch generated in this fishery, and they comprise a significant proportion of the seabird guild behind trawl boats (N. Brothers pers. comm.). Five to 18% of the fish identified (by number) in the diet samples were thought to have originated in this manner. Whiptails, Cardinalfish, Sawbellies, Perch and Snappers are deepwater species that are known to be taken in the by-catch of trawlers within the region (Last et al. 1983). The 18% estimate was derived from the stomach samples, and while the prevalence of large, robust Whiptail otoliths in these samples (which would have accumulated over time) would tend to have inflated the importance of by-catch species, the 5% estimate derived from the fresh samples is probably understated. A number of intact fresh fish could not be identified, and these along with a proportion of the fresh fish that lacked diagnostic remains, did not appear to be amongst the usual prey items. While this does not necessarily indicate that they were trawler discards, it does leave room for error.

The situation for squid is less clear. Generally less is known of the habits of squids, and despite ecological information for some groups, squid availability to albatrosses is further complicated because some species float while others sink after death, and this characteristic is not known for all Family groups (Lipinski & Jackson 1989, Croxall & Prince 1994). Of the species consumed by Shy albatrosses, the Sepiids, Histioteuthids, Cranchiids, and Mastigoteuthids are thought to float, while the Ommastrephids, Octopuses, and Onychoteuthids are thought to sink (Lipinski & Jackson 1989). The designation for *Moroteuthis ingens* (an Onychoteuthid) however, is questionable, and Lipinski & Jackson (1989) suspected that it may float after death. The large size of beaks indicates that the *Moroteuthis ingens* consumed by Shy albatrosses were mature, and this along with the importance of this species in the diet of Wandering albatrosses at Crozet Island (Weimerskirch et al. 1997b) seems to indicate that adult animals are available at or near the surface. Similar to other species of *Thalassarche* albatrosses, Shy albatrosses are significant consumers of juvenile Ommastrephids (Gould's squid) during the breeding season (Croxall & Prince 1994, Cherel & Klages 1998). Using this information, and assuming conservatively that the squids for which floating/sinking status is unknown (Argonauts, Cycloteuthids, Enoploteuthids) were also taken as by-catch, it seems unlikely that more than 3% (53 of 1752) of the squid would have originated as fisheries waste.

Reid et al. (1996) comment upon the abundance of bentho-pelagic fish (those likely to have been taken as trawler discards) to the diet of Black-browed and Grey-headed albatrosses at South Georgia in years with and without the presence of a trawl fishery

operating within their foraging grounds. The bentho-pelagic fish *Patagonotothen guntheri* contributed 51% and 11% by mass to the fish portion of the diet of Black-browed and Grey-headed albatrosses when the fishery was operating, while it was not observed in the diet when the fishery was absent. The only other studies detailing the use of fisheries discards are Thompson's (1992) and Thompson & Riddy's (1995) studies of Black-browed albatrosses in the Falkland Islands. Waste from the *Loligo gahi* trawl fishery was estimated to provide 10-15% of the total food requirements of breeding Black-browed albatrosses during the chick-rearing period (Thompson 1992). A later study in the same region, estimated that offal and discards from "finfish" trawlers would have provided up to 4.4% of the estimated annual energy requirements of the breeding Black-browed albatrosses (Thompson & Riddy 1995). As these trawl fisheries are larger predators of both "finfish" and squid than were the albatrosses prior to their commencement, they are expected to have long-term detrimental effects on the squid and finfish, as well as the albatross populations. Apart from providing an unnatural food source, and potentially threatening the natural prey base, the discharge of fisheries waste at sea increases the attractiveness of boats to birds, which ultimately leads to their high rates of incidental mortality in both trawl and longline fisheries (Bartle 1991, Brothers 1991, Gales et al. 1998).

Jack mackerel and Gould's squid are also the targets of commercial fisheries in Tasmania. A large volume purse-seine fishery targeting surface or near surface schools of Jack mackerel commenced in 1985, and it has taken between 10,000 and 42,000 tonnes annually since that time (McLoughlin et al. 1995). The fishery runs from October to May, with as much as 95% coming from eastern Tasmanian State waters (McLoughlin et al. 1995). The majority of the fish range between 25-37 cm in fork length (Williams et al. 1989), and are primarily used to produce fishmeal for livestock and aquaculture feeds, while some are used for bait in the local longline and Rock lobster *Jasus edwardsii* fisheries (Kailola et al. 1993). Very little of the fish is used for human consumption (Kailola et al. 1993). Redbait is one of the major by-catch species in this fishery, constituting up to 30% of the fish taken in some hauls (Williams & Pullen 1993).

There is a relatively small jig fishery for Gould's squid in western Bass Strait. Previous fishing efforts, however, indicate that major concentrations of squid are available in the area (Kailola et al. 1993). While the annual catch in this fishery has been just a couple of hundred tonnes since the mid-1980's, a catch of 1,800 tonnes in 1995 has seen renewed interest in the fishery (McLoughlin et al. 1997, Lister 1998). Fisheries management authorities regard the stock as underexploited, and there are calls for further fishery

development (McLoughlin et al. 1997).

There is overlap in the size of Jack mackerel taken both by the albatrosses and New Zealand fur seals with the commercial fisheries (Table 6.13). However, despite size correspondence or the lack of it, the overall importance of Jack mackerel, Redbait and Gould's squid to all large homeothermic marine predators in the Tasmanian region clearly indicates that either failure to account for predator requirements, or commercial overexploitation of any of these species, would have detrimental impacts upon the predator populations (Brothers et al. 1993, Gales et al. 1993, Gales & Pemberton 1994, Lake 1997). The food requirements of all of these predators must be considered if these species are to be managed in an ecologically sustainable manner.

Appendix 6A: Conversion formulae used for estimating the sizes of prey consumed by Shy albatrosses. Mantle (ML) and fork lengths (FL) are given in mm, except for Jack mackerel and Redbait where the units are cm, and weights (W) are stated in grams. LRL is lower rostral length, HL is lower hood length, CL is crest length, and OL is otolith length. Where available the size range of specimens used to calculate the regression equations are shown.

Cephalopods:	ML	W	Equation reliability (Source)
1. *Nototodarus gouldi*	ML= 38 x [(LRL)+0.71] (ML range=78 - 401)	log W= 1.735 x 10^{-5}+3.089log(ML)** (Mass range ≈ 10 - 1500)	Species-specific (O'Sullivan & Cullen 1983)
2. *Sepiid spp.*	ML= -2.14 + 21.89(HL)	ln W= -2.09 + 4.06 ln(HL)	Genus (Clarke 1986)
3. *Octopoteuthis spp.*	ML= -0.4 + 17.3(LRL)	ln W= 0.166 + 2.31 ln(LRL)	Genus (Clarke 1986)
4. *Moroteuthis ingens*	ML= 39.61(LRL) - 13.58 (r^2=0.92, n=137, ML range=145 - 520)	log W= 2.53logLRL + 0.69** (Mass range=128-5014)	Species-specific (Jackson 1995)
5. *Octopod spp.*	ML= 5.39 + 24.9(CL)	ln W= 1.82 + 3.03 ln(HL)	Genus (Clarke 1986)
6. *Argonauta nodosa*	ML= -7.70 + 7.19(CL)	log W= -2.97 + 2.62 log (ML)	Species-specific (Clarke, unpubl. cited in Gales et al. 1993)
7. *Teuthowenia spp.*	ML= 12.2 + 40.78(LRL)	ln W= 0.728 + 2.34 ln(LRL)	Genus (Clarke 1986)
8. *Histioteuthis spp.*	ML = -13.6 + 22.21(LRL)	ln W= 1.594 +2.31 ln(LRL)	Family (Clarke 1986)
9. *Cycloteuthis sirventi*	ML= 31(LRL)	ln W= 1.89 + 1.95 ln(LRL)	Species-specific (Clarke 1986)
10.*Ancistrocheirus lesueri*	ML= -41.3 + 40.75(LRL)	ln W= -0.194 + 3.56 ln(LRL)	Species-specific (Clarke 1986)
11. *Mastigoteuthis spp.*	ML= -1.8 + 29.08(LRL)	ln W= 0.184 + 2.88 ln(LRL)	Genus (Clarke 1986)

**average of equations for males and females.

Fish:	FL	W	Equation reliability (Source)
1. *Trachurus declivis*	FL= -4.77 + 3.864E-3 x (OLμm) (r^2=0.922, n=2488, FL range=6.7-44.0)	Log(W)=-13.104 + 3.953 x log (OLμm) (r^2=0.938, n=2488, W range=3-990)	Species-specific (H. Williams and G. Pullen unpubl. data, cited in Gales & Pemberton 1994, Corrigendum 45: 1367)
2. *Emmelichthys nitidus*	FL=-3.494 + 3.565E-3 x (OLμm) (r^2=0.961, n=406, FL range=10.4-30.5)	Log(W, g)=-13.872 + 4.154 x log (OL μm) (r^2=0.959, n=406, W range=12-377)	Species-specific (H. Williams and G. Pullen unpubl. data, cited in Gales & Pemberton 1994; Corrigendum 45: 1367)
3. *Thyrsites atun*	FL=22.06 x $OL^{1.42}$ (r^2=0.95, n=25, FL range=173-1015)	W(g)=2.3 x $10^{-6}FL^{3.10}$ (r^2=1.00, n=54, FL range =108-1015)	Species-specific (Gales & Pemberton 1990)

Appendix 6B: Percent frequency of occurrence (FOO%), and percent numerical abundance for the species and taxa identified in the fresh food samples from Shy albatross chicks at Albatross Island, Tasmania, 1996/97 and 1997/98. Figures include only fresh prey items.

Sampling Period	February 1997		April 1997		February 1998		April 1998	
n with identifiable prey	23		16		21		21	
number of identified prey	1053		31		321		91	
	FOO%	n (%)	FOO%	n (%)	FOO%	n (%)	FOO %	n (%)
Fish								
Carangidae								
Trachurus declivis	47.8	15 (1.4)	68.8	16 (51.6)	47.6	12 (3.7)	57.1	14 (15.4)
Carangid spp.	-	-	6.3	1 (3.2)	9.5	2 (0.6)	4.8	1 (1.1)
Emmelichthyidae								
Emmelichthys nitidus	21.7	10 (1.0)	-	-	-	-	4.8	4 (4.4)
Moridae								
Pseudophycis bachus	4.3	1 (< 0.1)	-	-	4.8	1 (0.3)	4.8	1 (4.8)
Macrouridae								
Coelorinchus australis	4.3	1 (< 0.1)	-	-	-	-	-	-
Gempylidae								
Thyrsites atun	-	-	6.3	1 (3.2)	9.5	2 (0.6)	-	-
Apogonidae								
Epiogonus lenimen	-	-	-	-	4.8	1 (0.3)	-	-
Latridae	4.3	1 (< 0.1)	6.3	1 (3.2)	-	-	-	-
Serranidae	-	-	6.3	1 (3.2)	4.8	1 (0.3)	-	-
Unidentified species	8.6	2 (0.2)	-	-	-	-	4.8	1 (1.1)
Squid (Total)								
Ommastrephidae								
Nototodarus gouldi	17.4	4 (0.4)	12.5	2 (6.5)	33.3	14 (4.4)	4.8	1 (4.8)
Sepiidae								
Sepia apama	-	-	6.3	1 (3.2)	-	-	9.5	2 (9.5)
Argonautidae								
Argonauta nodosa	4.3	1 (<0.1)	-	-	-	-	-	-
Unidentified species	-	-	-	-	-	-	-	-
Crustaceans								
Euphausiacea								
Nyctiphanes australis	47.8	966 (91.7)	-	-	-	-	-	-
Isopoda	4.3	2 (0.2)	6.3	2 (6.5)	4.8	3 (0.9)	-	-
Unidentified species	-	-	-	-	-	-	-	-
Tunicates (Total)								
Pyrosomatidae								
Pyrosomas spp.	34.5	46 (4.4)	12.5	6 (19.4)	81.0	285 (88.8)	42.9	68 (74.7)

Appendix 6C: Percent frequency of occurrence (FOO%), and percent numerical abundance of the species and taxa identified in the whole stomach samples from dead Shy albatross chicks at Albatross Island, Tasmania, 1994/95 to 1997/98

A. Fledging (April only) 1994/95 and 1995/96

	April 1995		December 1995		February 1996		April 1996	
n with identified prey	56		9		84		101	
n of identified prey	432		37		631		1368	
	FOO%	n(%)	FOO%	n(%)	FOO%	n(%)	FOO%	n(%)
Fish								
Carangidae								
Trachurus declivis	7.1	5 (1.2)	-	-	3.6	4 (0.6)	3.0	3 (0.2)
Carangid spp.	3.6	2 (0.5)	-	-	1.2	1 (0.2)	-	-
Emmelichthyidae								
Emmelichthys nitidus	8.9	19 (4.4)	-	-	1.2	1 (0.2)	1.0	1 (<0.1)
Moridae								
Pseudophycis bachus	-	-	-	-	3.6	3 (0.5)	3.0	3 (0.2)
Macrouridae								
Unidentified whiptail	-	-	-	-	1.2	1 (0.2)	-	-
Berycidae								
Centroberyx spp.	-	-	-	-	1.2	1 (0.2)	-	-
Clupeidae	1.8	1 (0.2)	-	-	-	-	-	-
Merlucciidae	1.8	1 (0.2)	-	-	-	-	-	-
Mugilidae	-	-	11.1	2 (5.4)	-	-	-	-
Platycephalidae	-	-	-	-	-	-	-	-
Trachichthyidae	-	-	-	-	1.2	1 (0.2)	-	-
Unidentified fish	-	-	-	-	-	-	-	-
Squids								
Ommastrephidae								
Nototodarus gouldi	83.9	245 (56.7)	100	32 (86.5)	76.2	145 (23.0)	84.2	201 (14.7)
Sepiidae								
Sepia apama	25.0	17 (3.9)	-	-	25.0	23 (3.6)	37.6	49 (3.6)
Sepia novaehollandiae	37.5	41 (9.5)	-	-	39.3	49 (7.8)	66.3	119 (8.7)
Sepia spp.	3.6	2 (0.5)	-	-	1.2	1 (0.2)	5.9	6 (0.4)
Octopoteuthidae								
Octopoteuthis spp.	7.1	4 (0.9)	-	-	3.6	3 (0.5)	3.0	3 (0.2)
Onychoteuthidae								
Moroteuthis ingens	-	-	-	-	-	-	45.0	6 (0.4)
Cranchiidae								
Teuthowenia cf megalops	3.6	2 (0.5)	-	-	1.2	2 (0.3)	-	-
Teuthowenia pellucida	-	-	-	-	-	-	-	-
Histioteuthidae								
Histioteuthis B4	-	-	-	-	-	-	1.0	2 (0.1)
Histioteuthis? celetaria	-	-	-	-	-	-	-	-
Octopodidae								
Octopus australis	-	-	-	-	-	-	2.0	3 (0.2)
Octopus spp.	1.6	1 (0.2)	-	-	1.2	1 (0.2)	1.0	1 (<0.1)
Argonautidae								
Argonauta nodosa	14.3	8 (1.9)	-	-	-	-	1.0	1 (<0.1)
Cycloteuthidae								
Cycloteuthis sirventi	-	-	-	-	-	-	-	-
Enoploteuthidae								
Ancistrocheirus lesueri	-	-	-	-	1.2	1 (0.2)	-	-
Mastigoteuthidae								
Mastigoteuthis spp.	-	-	-	-	-	-	-	-
Unidentified cephalopods	-	-	-	-	-	-	-	-
Crustaceans								
Cirripedia								
Lepadomorpha	-	-	-	-	-	-	-	-
Euphausiacea								
Nyctiphanes australis	-	-	-	-	-	-	-	-
Isopoda	-	-	22.2	3 (8.1)	1.2	1 (0.2)	2.0	2 (0.1)
Decapoda								
Unidentified decapod	-	-	-	-	2.4	2 (0.3)	1.0	1 (<0.1)
Unknown crustaceans	-	-	-	-	1.2	1 (0.2)	-	-
Tunicates								
Pyrosomatidae								
Pyrosomas spp.	21.4	85 (19.7)	-	-	54.6	390 (61.8)	84.2	967 (70.7)

B. 1996/97 Season

	December 1996		February 1997		April 1997	
n with identified prey	22		53		57	
n of identified prey	252		212		311	
	FOO%	n(%)	FOO%	n(%)	FOO%	n(%)
Fish						
Carangidae						
Trachurus declivis	-	-	1.9	1 (0.5)	3.5	2 (0.6)
Carangid spp.	4.5	1 (0.4)	3.8	2 (0.9)	1.8	1 (0.3)
Emmelichthyidae						
Emmelichthys nitidus	4.5	1 (0.4)	1.9	2 (0.9)	-	-
Moridae						
Pseudophycis bachus	-	-	1.9	1 (0.5)	-	-
Macrouridae						
Unidentified whiptail	4.5	1 (0.4)	3.8	2 (0.9)	1.8	1 (0.3)
Berycidae						
Centroberyx spp.	-	-	-	-	-	-
Clupeidae	-	-	-	-	-	-
Merlucciidae	4.5	1 (0.4)	-	-	-	-
Mugilidae	-	-	-	-	-	-
Platycephalidae	-	-	-	-	-	-
Trachichthyidae	-	-	-	-	-	-
Unidentified fish	-	-	-	-	-	-
Squids						
Ommastrephidae						
Nototodarus gouldi	63.6	16 (6.3)	84.9	110 (51.9)	82.5	127 (40.8)
Sepiidae						
Sepia apama	4.5	1 (0.4)	17.0	10 (4.7)	21.1	14 (4.5)
Sepia novaehollandiae	9.1	2 (0.8)	15.1	10 (4.7)	31.6	22 (7.1)
Sepia spp.	4.5	1 (0.4)	5.7	3 (1.4)	7.0	4 (1.3)
Octopoteuthidae						
Octopoteuthis spp.	4.5	1 (0.4)	7.5	4 (1.9)	5.3	3 (1.0)
Onychoteuthidae						
Moroteuthis ingens	-	-	1.9	1 (0.5)	1.8	1 (0.3)
Cranchiidae						
Teuthowenia cf megalops	-	-	1.9	1 (0.5)	-	-
Teuthowenia pellucida	-	-	-	-	-	-
Histioteuthidae						
Histioteuthis B4	-	-	1.9	1 (0.5)	-	-
Histioteuthis? celetaria	-	-	1.9	1 (0.5)	-	-
Octopodidae						
Octopus australis	-	-	3.8	2 (0.9)	-	-
Octopus spp.	-	-	-	-	3.5	6 (1.9)
Argonautidae						
Argonauta nodosa	-	-	7.5	4 (1.9)	21.1	13 (4.2)
Cycloteuthidae						
Cycloteuthis sirventi	-	-	-	-	-	-
Enoploteuthidae						
Ancistrocheirus lesueri	-	-	-	-	-	-
Mastigoteuthidae						
Mastigoteuthis spp.	-	-	-	-	-	-
Unidentified cephalopods	4.5	1 (0.4)	1.9	1 (0.5)	-	-
Crustaceans						
Cirripedia						
Lepadomorpha	-	-	1.9	1 (0.5)	-	-
Euphausiacea						
Nyctiphanes australis	22.7	220 (87.3)	3.8	3 (1.4)	-	-
Isopoda	9.1	2 (0.8)	-	-	-	-
Decapoda						
Unidentified decapod	-	-	-	-	-	-
Unknown crustaceans	-	-	-	-	-	-
Tunicates						
Pyrosomatidae						
Pyrosomas spp.	9.1	4 (1.6)	22.6	52 (24.5)	47.4	117 (37.6)

C. 1997/98 Season

	January 1998		February 1998		April 1998	
n with identified prey	18		55		48	
n of identified prey	639		3394		1284	
	FOO%	n(%)	FOO%	n(%)	FOO%	n(%)
Fish						
Carangidae						
Trachurus declivis	-	-	12.7	7 (0.2)	4.2	2 (0.2)
Carangid spp.	-	-	-	-	2.1	1 (<0.1)
Emmelichthyidae						
Emmelichthys nitidus	5.6	2 (0.3)	-	-	-	-
Moridae						
Pseudophycis bachus	-	-	-	-	8.3	4 (0.3)
Macrouridae						
Unidentified whiptail	11.1	4 (0.6)	5.5	4 (0.1)	-	-
Berycidae						
Centroberyx spp.	-	-	-	-	-	-
Clupeidae	-	-	-	-	-	-
Merlucciidae	-	-	-	-	-	-
Mugilidae	-	-	-	-	-	-
Platycephalidae	5.6	1 (0.2)	-	-	-	-
Trachichthyidae	-	-	-	-	-	-
Unidentified fish	-	-	1.8	1 (<0.1)	-	-
Squids						
Ommastrephidae						
Nototodarus gouldi	88.9	44 (6.9)	89.1	131 (3.9)	66.7	83 (6.5)
Sepiidae						
Sepia apama	22.2	4 (0.6)	25.5	14 (0.4)	52.1	37 (2.9)
Sepia novaehollandiae	-	-	23.6	16 (0.5)	45.8	38 (3.0)
Sepia spp.	5.6	1 (0.2)	-	-	10.4	5 (0.4)
Octopoteuthidae						
Octopoteuthis spp.	-	-	7.3	4 (0.1)	6.3	3 (0.2)
Onychoteuthidae						
Moroteuthis ingens	-	-	3.6	2 (<0.1)	2.1	1 (<0.1)
Cranchiidae						
Teuthowenia cf megalops	-	-	1.8	2 (<0.1)	-	-
Teuthowenia pellucida	5.6	1 (0.2)	-	-	-	-
Histioteuthidae						
Histioteuthis B4	-	-	-	-	-	-
Histioteuthis? celetaria	-	-	-	-	-	-
Octopodidae						
Octopus australis	11.1	2 (0.3)	3.6	2 (<0.1)	2.1	1 (<0.1)
Octopus spp.	-	-	-	-	10.4	5 (0.4)
Argonautidae						
Argonauta nodosa	-	-	-	-	-	-
Cycloteuthidae						
Cycloteuthis sirventi	-	-	-	-	2.1	1 (<0.1)
Enoploteuthidae						
Ancistrocheirus lesueri	-	-	-	-	-	-
Mastigoteuthidae						
Mastigoteuthis spp.	-	-	1.8	1 (<0.1)	-	-
Unidentified cephalopods	11.1	4 (0.6)	5.5	4 (0.1)	2.1	1 (<0.1)
Crustaceans						
Cirripedia						
Lepadomorpha	-	-	-	-	-	-
Euphausiacea						
Nyctiphanes australis	-	-	-	-	2.1	1 (<0.1)
Isopoda	-	-	5.5	4 (0.1)	-	-
Decapoda						
Unidentified decapod	-	-	1.8	1 (<0.1)	2.1	1 (<0.1)
Unknown crustaceans	-	-	-	-		
Tunicates						
Pyrosomatidae						
Pyrosomas spp.	63.6	576 (90.1)	100	3201 (94.3)	97.9	1100 (85.7)

Chapter 7

PROVISIONING AND GROWTH RATES OF SHY ALBATROSSES *Thalassarche cauta* BREEDING IN AUSTRALIA

7.1 INTRODUCTION

All Procellariiforme seabirds have a number of life history characteristics in common; delayed onset of maturity, low reproductive output, long life spans, and slow post-natal development (Lack 1968). Emergence of these characteristics across the Order, and in seabirds in general, is thought to be driven by the general unpredictability of food resources, and the spatial separation of the breeding and feeding grounds (Ashmole 1971). However, even within the Procellariiformes, species specific interactions with the marine environment vary enormously, and these have resulted in a wide variety of adult foraging and chick-provisioning strategies.

In the literature describing Procellariiforme provisioning regimes, much recent attention has focused on two related issues. First, why albatrosses and petrels provision their chicks to the extent that they reach a mass well in excess of the adults, and second, whether parents have the capacity to regulate the rate of food delivery to their chicks (e.g., Ricklefs 1992, Ricklefs & Schew 1994, Bolton 1995, Weimerskirch et al. 1995, Lorentsen 1996, Hamer & Thompson 1997, Hamer et al. 1997). While regulation capacity was examined only secondarily in many of these studies, it is the more relevant focus here. Results of previous work examining regulation capacity have been variable, some studies have found that parents could alter provisioning schedules according to chick needs (Bolton 1995, Weimerskirch et al. 1995, Hamer & Thompson 1997), while others found adults to be unresponsive (Ricklefs 1987 & 1992, Lorentsen 1996, Thompson et al. 1997). Although the presence of a single mechanism controlling provisioning capacity across the Order seems highly unlikely, several explanations have been proposed for its absence. These include: (1) that adults are unable to detect the nutritional status of their chicks, (2) if chick nutritional status can be detected, parents are either unwilling or unable (because of their foraging strategy) to alter provisioning schedules, and (3) adults may have an intrinsic feeding rhythm, which is independent of chick requirements (e.g., Ricklefs 1987).

For many species provisioning performance has been described solely from repeated

chick weighings. Recent work with pelagic Procellariiformes, however, has highlighted the importance of working instead at the level of the individual parent (Chaurand & Weimerskirch 1994b,Weimerskirch et al. 1994 & 1995, Weimerskirch 1998a). When raising chicks, pelagic species studied to date either alternate (Blue petrels *Halobaena caerulea*, and Thin-billed prions *Pachyptila belcheri*) or mix (Wandering *Diomedea exulans* and Yellow nosed *Thalassarche chlororhynchos* albatrosses, Sooty *Puffinus griseus* and Short-tailed shearwaters *P. tenuirostris*) short foraging trips over the continental shelf with longer trips into pelagic waters (Chaurand & Weimerskirch 1994, Weimerskirch et al. 1994, 1995, 1997b &1997c, Klomp & Schultz 1998, Weimerskirch 1998a). The decision to undertake a short or long trip and hence the frequency at which to provision the offspring appears, for these species, to be primarily determined by adult body condition. While short trips increase the energy flow to the chick, they are reported to be at the expense of adult body condition, as adults tend to lose mass. Long foraging trips are undertaken when adults are in poor condition, and while energy flow to the chick is reduced, they are able to regain the mass lost on short trips (Chaurand & Weimerskirch 1994, Weimerskirch et al. 1994, 1995, 1997b, 1997c, Klomp & Schultz 1998, Weimerskirch 1998a). This two-fold strategy appears to be a compromise between meeting the high energy requirements of the chick (Weimerskirch et al. 1994), and the prudence of the parents in never allowing body reserves to deteriorate below threshold (Drent & Dann 1980).

It has been proposed that this dual strategy offers pelagic species greater flexibility (relative to neritic species) in responding to chick demands, as provisioning rates could be increased by increasing the proportion of time spent in short foraging trips (Weimerskirch et al. 1995 & 1997c). On this premise, Black-browed albatrosses *Thalassarche melanophris* at Kerguelen Island, which undertake only short foraging trips while raising chicks, were suggested to have limited regulation capacity (Weimerskirch et al. 1997c). In support of this, adult Black-browed albatrosses responded to experimentally over-fed chicks by decreasing food delivery rates, but they could not increase delivery rates when their chicks were underfed (Weimerskirch et al. 1997c). While adult body mass varied through time, the extent of the mass change did not influence either the subsequent foraging trip duration or the size of the meal next delivered to the chick. While body condition exerts control over breeding decisions for pelagic species, it appears not to do so for the neritic species studied to date (Chastel et al. 1995a & 1995b).

Engineered by Prince & Walton (1984), and since used extensively by Prince et al. (submitted), automatic weighing platforms have revolutionized remote collection of

provisioning and growth information from albatrosses. When used concurrent with telemetry receiving systems (to obtain information on individual adult attendance patterns), detailed sets of adult provisioning and chick growth data result. Such information is now available for Black-browed, Grey-headed *Thalassarche chrysostoma* (Prince et al. submitted) and Yellow-nosed albatrosses (Weimerskirch & Prince unpubl. data), and we present results here for Shy albatrosses *Thalassarche cauta* in Tasmania.

Shy albatrosses are a neritic feeding species with an approximate 300 km foraging range over the southeast Australian continental shelf during the breeding season (Brothers et al. 1998, and Chapters 3 & 8). Birds undertake short foraging trips (averaging 1-3 days) throughout the chick-rearing period (Chapter 5). This study spans three consecutive breeding seasons (1995/96 to 1997/98) and quantifies natural variation in provisioning and growth rates between years. Whenever possible the same breeding pairs were studied across years. These data were used to:

(1) describe the provisioning patterns (including meal sizes, chick fasting intervals and overall provisioning rates) and growth rates of chicks across the rearing period;

(2) compare provisioning and growth rates of male and female chicks;

(3) explore sex differences in adult provisioning performance;

(4) assess the species natural ability to regulate food delivery to chicks;

(5) determine the influence of adult provisioning performance on the growth rates of chicks.

7.2 METHODS

7.2.1 *Species and study site*

Recent revisions to albatross taxonomy have elevated the populations of Shy albatrosses breeding in Australia to full species status (Nunn et al. 1996, Robertson & Nunn 1998). The species breeds on three islands off Tasmania; Albatross Island (40° 24'S, 144° 32'E) in western Bass Strait, and Pedra Branca (43° 52'S, 146° 58'E) and Mewstone (43.742°S, 146.375°E) off Tasmania's south coast. Breeding is annual, beginning when birds are 5 years of age (N. Brothers unpubl. data). Egg laying commences in September, with parents taking alternate shifts on the egg until hatching in December. Young chicks are brooded, again by both parents, over the next 3-4 weeks, and are left alone at the nest

between late December and early January. The post-brood period of parental care continues for another 14-16 weeks. The earliest chicks leave the colonies late March and fledging continues throughout April. Young birds spend at least two years at sea before returning to their natal colonies.

7.2.2 *Data collection*

Information on individual adult provisioning performance and chick growth rates was collected at Albatross Island between 1995/96 and 1997/98. Albatross Island has four separate breeding colonies (the North, Main, South and West), each with it's own characteristic breeding success rate, that tends to be relatively stable between years (N. Brothers unpubl. data). This study was conducted in the North colony, and comparisons of breeding success between study and control nests were conducted within this colony.

Chick masses were collected remotely using automatic nest platforms (Francis Scientific Instruments, Cambridge, UK) and parental attendance in the colony was recorded using a remote telemetry recording system (Sirtrack, Havelock North, New Zealand; Advanced Telemetry Systems, Isanti, MN, USA, respectively). Combining the chick mass and adult attendance records enabled each chick feeding event to be attributed to one of its parents.

To minimize their size and bulk, VHF transmitters were packaged with an internal loop antennae, and they had a range of 150 m. The transmitters weighed 16 g, and after being sewn into padded Velcro bands secured with quick setting epoxy (Five minute Araldite) and cable ties, the final package weighed 20-21 g (45.5 mm high x 23.0 mm wide x 38.9 mm long, 0.4-0.6% adult body mass). Transmitters were placed on each member of each breeding pair (on the right leg) as they either incubated or brooded their chick. Adults were also banded with a stainless steel band on the left leg and colour marked with an individually identifiable pattern on the breast. To reduce disturbance during the breeding season, the sex of each adult was determined during the subsequent winter period using morphometric indices (Hedd et al. 1998, and Chapter 2). Transmitters were also then removed from the birds and repowered for the next breeding season.

Five automatic nest platforms were set into position at the end of the brood/guard period in December 1995/January 1996. The original nest of each pair was carefully removed and replaced with an artificial nest. During the 30 minutes it took to install the platforms, chicks were placed either in a box or in an unoccupied adjacent nest. The artificial nests consisted of a fiberglass bowl and base that housed a weighing platform (Figure 7.1). Chick masses were subsequently recorded (± 10 g) every 10 minutes until fledging, some

12-15 weeks later. Nests were calibrated using a series of 1 kg weights at the beginning of the post-brood period each season and again after the chicks had fledged. Nests were also tared post-fledging to obtain the mass of any accumulated nesting material, and chick masses were adjusted accordingly.

During each year, nest contents (i.e., live chick, dead chick or empty nest) were noted during brood/guard in December/January, at mid-chick rearing in February and again at fledging in April. In the final two years, chicks were stainless steel banded on the left leg and colour banded on the right leg in mid-February, so that they could be readily identified in the colony at fledging. The sex of study chicks was determined at fledging using morphometric measurements (Hedd et al. 1998, and Chapter 2). Any study chick that died prior to fledging was also dissected for sex confirmation and condition assessment. There is an avian pox viral infection prevalent at Albatross Island, and while its effects vary inter-annually, breeding success can be reduced as low as 10% in some colonies in some years (N. Brothers unpubl. data). All carcasses were assigned a qualitative condition score that ranged from 0-5; 0 indicated no fat accumulation while 5 indicated extensive subcutaneous and peritoneal fat reserves. The index was developed using 540 chicks that ranged from 250 to 5,250 g, and as such, it likely incorporated most possible conditions.

7.2.3 *Sampling protocols*

In order to obtain accurate meal size measurements and also to have the nests run for a sufficient period of time unattended in the field (40-50 days), chick mass was recorded at 10 minute intervals. After the end of the brooding period, adults visit the colony only briefly to feed their chick, sometimes departing within five minutes. Being conducted concurrently with a more extensive study of annual colony attendance patterns (Chapter 5), the cycle time of the telemetry system was approximately five minutes. Accepting that all meals received by chicks were delivered by their parents, just 12 of 1,226 (1%) meals were delivered without a parents presence being detected. In these instances adults presumably spent less than the five minutes required by the system to be recorded in the colony.

The aim was to longitudinally study the provisioning performance of the same five breeding pairs across three years. However, because of both natural breeding failures and the failure of some equipment this was not possible for all pairs. Four of the original five pairs were studied in all seasons (I3, R35, R45 and Z7, Table 7.1), but breeding failures

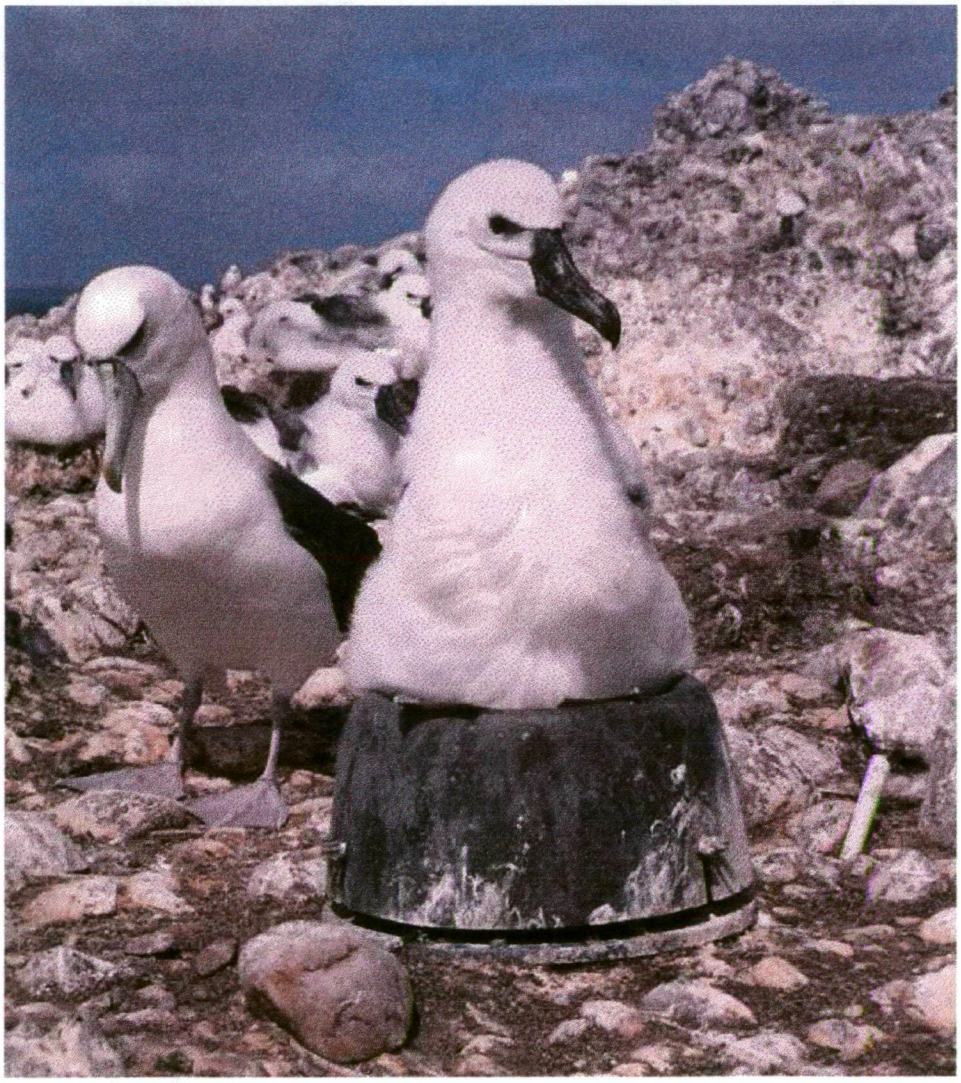


Figure 7.1: Shy albatross chick sitting in an automatic nest on Albatross Island

resulted in records being incomplete for two of these four pairs in two separate years (I3 in 1997/98 and R35 in 1996/97). The fifth original pair (Z6) was studied only during the first two years, and it's replacement (Z10) only in the last two years. Nest V5 was studied only in 1997/98. Provisioning data were never collected for the pair at Z10 because of mechanical problems in 1996/97, and breeding failure in 1997/98.

Three of the five initially selected pairs (R35, R45 and I3) had bred successfully in the previous eight years, and at least one member of each of these pairs was of known age (Table 7.2). Other suitably sized study (structurally large) nests were selected at random throughout the colony. While one of these nests contained a known age bird (male at nest V5), nothing was known of this birds breeding history.

Table 7.1: Details of the pairs of birds studied each year, along with outcomes of each breeding attempt (presence or absence of a fledgling).

	1995/96		1996/97		1997/98	
Nest	egg	fledgling	egg	Fledgling	Egg	Fledgling
R45	√	√	√	√	√	√
Z7	√	√	√	√	√	√
I3	√	√	√	√	√	X
R35	√	√	√	X	√	X
Z6	√	√	√	X	not monitored	
Z10	not monitored		√	√	√	X
V5	not monitored		not monitored		√	√

7.2.4 *Data Analysis*

7.2.4.1 *Chick Provisioning*

Meal sizes, chick fasting/adult feeding intervals, and overall provisioning rates were calculated from the mass records (an example of which is shown in Figure 7.2a). Meal sizes were calculated from rapid and sustained increases in chick body mass between successive readings (Figure 7.2b). Mass increments resulting from feeds were distinguishable from those resulting from precipitation, as the latter were progressive and/or they occurred simultaneously in all chicks. As meal sizes were calculated from relative as opposed to absolute changes in recorded mass, precipitation did not require adjustments to these calculations. Chick fasting intervals were calculated as the time elapsed between successive meals, while individual adult feeding intervals were calculated as the time elapsed between successive deliveries. Provisioning rates were calculated by summing the total amount of food received by the chick in a given period

(across 10 days for example, see below), divided by the intervening interval (10 days), and expressed in g/day. Data were tabulated and presented primarily from the chick's perspective (as the recipient of all food), but also from the perspective of each adult as an individual provider.

Table 7.2: Ages of adults at the study nests. Precisely known-aged birds were banded as chicks at the colony, while those indicated as x+ years old were banded as breeders, and assumed to have been 5+ years old at the time (the minimum recorded breeding age, N. Brothers, unpubl. data). Age was assigned from the year of fledging.

	1995/96		1996/97		1997/98	
Nest	Male	Female	Male	Female	Male	Female
I3	10	13	11	14	12	15
R35	11+	14	12+	15	13+	16
R45	-	14	-	15	-	16
V5	not monitored		not monitored		16	-
Z6	-	-	-	-	not monitored	
Z7	-	-	-	-	-	-
Z10	not monitored		-	-	-	-

These indices of provisioning performance (meal sizes, fasting/feeding intervals, and overall provisioning rates) were examined at two temporal scales:

1) across the chick-rearing period in 10 day blocks (with chicks from 20-29 days to fledging)

2) both prior and subsequent to the chicks attaining actual peak mass. The peak mass period was defined as the 10 day interval during which the chicks mass initially reached its maximum. Peak mass was reached when chicks were between 90-99 and 130-139 days of age.

Although the ages of chicks were not precisely known, they were estimated from chick size in early/mid-December in conjunction with the time that the duration of their parents shifts at the nest decreased to 24 hours (as in Chapter 5). For the single pair where hatching was observed (Chapter 5), shift durations decreased to 24 hours on the hatching day.

The temporal pattern of food delivery to chicks was examined daily throughout the rearing period relative to ambient light conditions. Each day was broken into four periods; daytime, nighttime, morning and evening twilight. Morning twilight commenced with the beginning of nautical twilight (defined as the instant when the

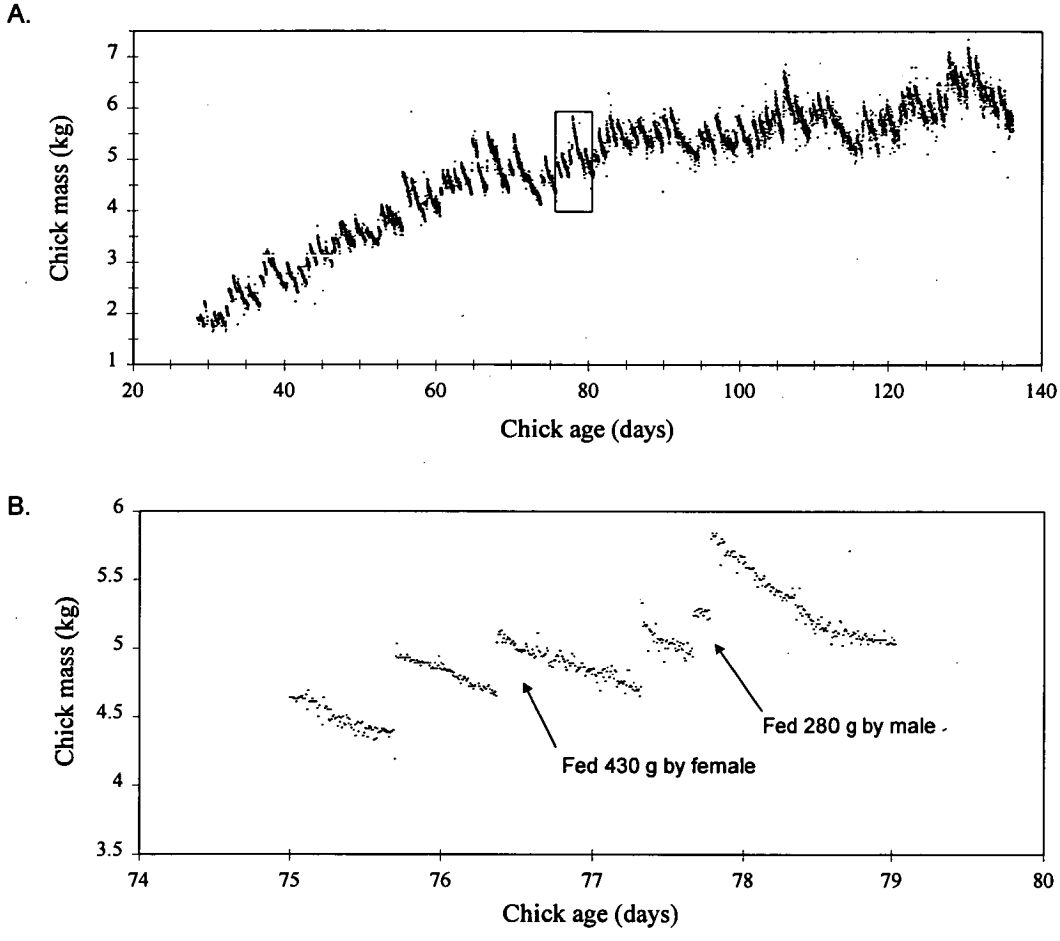


Figure 7.2: (A) Complete mass record of a Shy albatross chick obtained from the automatic weighing platforms between the end of the brooding period and fledging. (B) Example of the rapid and sustained mass increases used to characterize feeding events.

centre of the sun is at a depression angle of 12° below the horizon) and ended with sunrise, while the evening twilight period commenced with sunset, and continued until the sun was at a depression angle of 12° below the horizon. Daytime incorporated the period from sunrise to sunset and nighttime, the period from the end of nautical twilight in the evening until the beginning of nautical twilight the following morning.

To assess whether parents fed their chicks independently of one another, the proportion of days upon which chicks were fed by neither, one or both parents were compared with relative frequencies expected under a binomial distribution (Ricklefs et al. 1985). The expected frequencies, if parents feed independently, are given by $(1-p)^2$, $2p(1-p)$, and p^2, where p is the probability of a chick receiving a feed on a given day. Analyses were conducted separately for each year of the study. In 1995/96 chicks were fed on 353 of 459 adult days, giving a p of 0.769, in 1996 chicks were fed on 131 of 169 adult days, giving a p of 0.775, and in 1997/98 chicks were fed on 272 of 376 adult days giving a p of 0.723. In all years the observed and expected frequencies were significantly different (Table 7.3), suggesting that the food delivery regimes of breeding pairs were not independent. Given this non-independence, data were analyzed using the "nest" as the replicate unit as opposed to the individual birds.

Table 7.3: Expected and observed chick feeding frequencies. Expected values were calculated from a binomial distribution where independence of feeding by members of each breeding pair was assumed.

Year	Number of nests	Expected feeding frequency (fed by neither, one or both)	Observed feeding frequency (fed by neither, one or both)	χ^2 test, p level
1995/96	5	24, 163, 271	106, 222, 131	377.1 $p < 0.001$
1996/97	3	9, 59, 102	38, 87, 44	146.5 $p < 0.001$
1997/98	3	19, 108, 150	73, 137, 67	203.4 $p < 0.001$

The following hypotheses were tested:

1) Chick provisioning rate is constant throughout the season

For each parameter in turn (meal size, fasting interval, and overall provisioning rate), repeated measures analyses of variance (ANOVAs) were conducted to determine whether provisioning patterns varied with chick age, and polynomial contrasts were used to assess the nature of the changes through time (i.e., linear, quadratic, or polynomial). Because

some pairs were studied in more than one year (Table 7.1), analyses were conducted separately for each year to ensure statistical independence.

2) Chicks are provisioned equally prior to and after they reach peak mass

Repeated measures ANOVAs were again used for each parameter in turn (meal size, fasting interval and overall provisioning rate). Given that there were no inter-annual differences in any of the provisioning parameters (see below), data for these analyses were pooled across years.

3) Chicks are provisioned equally in all years

Inter-annual differences were assessed in two ways; first, analyses were limited to nests studied longitudinally, and second, data for all years were combined, despite the fact that some nests were represented in more than one year. Two-way repeated measures ANOVAs were used, for each parameter in turn (meal size, fasting interval and overall provisioning rate), with year as the between subjects factor.

4) Male and female chicks are provisioned equally

Chick sex was determined using morphometric indices during 1996/97 and 1997/98 (Hedd et al. 1998, and Chapter 2), and confirmed via dissection for three individuals (nest R35 in 1995/96, and nests I3 and Z7 in 1996/97). Data resulted for four male and three female chicks, with the sex of the remaining fledglings unknown. Again, as there were no inter-annual differences in the provisioning parameters (see below), the effect of chick sex was assessed using independent samples t-tests on average parameters across the season.

5) Provisioning rates are similar at successful and unsuccessful nests

Of the 13 chicks studied, just two died in their nests; the chick at nest R35 in 1996/97, and the chick at nest I3 in 1997/98. Three remaining chicks that left their nests, but which later died on the outskirts of the colony were, for these analyses, considered to have fledged successfully. As there were no inter-annual differences in the provisioning parameters (see below), data were pooled across years and analyzed with two-way repeated measures ANOVAs, using nest outcome (successful or unsuccessful attempt) as the between subjects factor. As repeated measures ANOVAs require no missing values, analyses were restricted to periods when chicks were aged 79 days and younger.

6) Male and female parents provision chicks equally well

A necessary precursor to testing this hypothesis was determining, for each parameter in turn (meal size, feeding interval and overall provisioning rate), if the response of males and females changed in a similar manner through time. This was assessed using a repeated measures ANOVA on gender difference scores (mean of the males score - mean of the females score). This condition satisfied, one-sample (paired) t-tests were used to evaluate whether the sexes actually differed (mean gender differences through time were evaluated against the null hypothesis that the mean difference was 0).

For all hypotheses aside from number 5, analyses were conducted only at nests where the chick fledged, and fledging was defined as the chicks nest departure and not its colony departure (as in Chapter 5). Most adults (65%) departed the colony prior to their chick leaving the nest, with 32% of the remainder making one additional visit, and just 9% making a second visit to the colony after the chick had left the nest. Chicks have been observed to leave their nests and solicit feeds from non-parents close to fledging, but the prevalence of this behaviour and the factors precipitating it (i.e. previous departure of their parents or not), have not been quantified.

7.2.4.1.1 Problems with interpretation and assumptions made of the attendance and provisioning data

Because of equipment malfunctions (mostly failing VHF transmitters), or combinations of failing equipment and early nest desertions, there were a number of gaps in the data. In some instances assumptions therefore had to be made prior to data analysis:

a) Each study bird carried a VHF transmitter. In instances where one transmitter from a pair failed, all feeds delivered to the nest in absence of the parent with the working transmitter were attributed to the parent carrying the failed transmitter. This situation occurred at nest R35 in 1995/96.

b) Some albatrosses deserted their chick part way through the rearing period, and did not return to the colony until the following winter (Chapter 5). Parents at two study nests deserted their chick during 1996/97 (the male at nest R45 shortly after the end of the brooding period (January), and the female at nest I3 in mid-February, when the chick was approximately six weeks from fledging). At nest R45 the female delivered all feeds to the chick over the next nine weeks, until early March, when her transmitter stopped working. In the intervening three weeks until fledging, all meals were assumed to have been delivered by the female. Similarly, following the females desertion at nest I3, the male was known to have fed the chick alone over the next three weeks, after which his

transmitter also stopped working. The male was assumed to have delivered the remainder of the feeds to fledging.

c) In cases where chicks were fed without their parents being recorded in the colony, the feeds were labeled 'unknown' origin. Neither foraging trip durations nor chick feeding intervals were calculated for the subsequent visit by either parent.

d) The chick at nest Z6 in 1995/96 was sitting outside its nest from 48 to 51 days of age. It was fed by both of its parents during this time, and the sizes of these meals were assumed to equal the average size of other meals delivered by these individuals during the appropriate 10 day period.

e) Finally, late in January 1997 the memory of the telemetry system filled and no attendance data were collected (between 28 January to 2 February 1997). It was not possible to attribute meals to individual parents during this time.

7.2.4.2 *Chick Growth*

7.2.4.2.1 Description of chick growth

For each chick on each day, the 0400 h mass was extracted from the 10 minute records (0400 h being the time furthest away from feeds delivered the previous day and therefore least likely to be influenced by food still residing in the chicks stomach). To avoid any disturbance to the adults, chicks were not weighed during the brood/guard period, resulting in initial masses when chicks were between 19 and 37 days old. The mean hatching mass (187 ± 23.1 g, n=43, N. Brothers unpubl. data) of other chicks at this site was added into the data set for each chick on the estimated hatching day. Standard equations (Gompertz, Richard's and von Bertalanffy) were used to explore the shape of the growth curve for each chick, and in all instances the Gompertz model provided the best fit to the data, yielding both the highest r^2 values and the most appropriate normal probability plots. Gompertz growth curves are of the following form:

$Mass=A*\exp(-\exp(-k*(age-t_i)))$, where

A= asymptotic mass in kilograms

k= growth constant in kilograms/day

t_i= the inflection point, or the age at maximum growth

Growth parameters were estimated separately for each chick, and also pooled to construct a generalized growth curve for the species. Growth indices were compared with other species, however, detailed Gompertz analyses were available only for Black-browed, and Grey-headed albatrosses (Ricketts & Prince 1981, Prince et al. submitted). Broader inter-specific comparisons were made by using the Gompertz curves to calculate t_{10}-t_{90} for Shy albatrosses, the period of time required for the chick to grow from 10% to 90% of asymptotic mass (Ricklefs 1968, Croxall 1984).

Average growth rates (g/day) were also calculated for each chick across the rearing period from the start of the study until both peak mass and fledging. Variation in growth rates between years and between the sexes were assessed using independent samples t-tests.

7.2.4.3 *Influence of provisioning on chick growth parameters*

Multiple regression techniques were employed to determine the influence, as well as the relative importance, of the different provisioning parameters (total food received, provisioning rate, number of meals, average meal size and average chick fasting intervals) on chick growth rates. Analyses were conducted using growth rates to both peak mass and to fledging.

Analyses were conducted using Statistica (release 4.5, StatSoft Inc.), and data are presented as means ± 1 S.D.

7.3 RESULTS

7.3.1 *General description of the data*

In late December 1995/early January 1996, five automatic nest platforms were placed under chicks that ranged from 28 to 37 days old. Full weight records were obtained for all five of these chicks through to fledging, but the chick from nest R35 died some days later before departing the colony. During 1996/97 four of the five nests operated and complete records were obtained for three fledglings. The fourth chick (again at R35), died in the nest late March, approximately one week before fledging commenced. A further two of the three fledglings from this season were found dead on the outskirts of the colony, after apparently trying to fly. Four nests were again operational in 1997/98 and three chicks fledged. The fourth chick (at nest I3) died in early March, when it was approximately 95 days old.

The hatching success (proportion of eggs that hatched), fledging success (proportion of hatched chicks that fledged) and overall breeding success (proportion of eggs that produced fledglings), was higher at study nests than for nests in the North colony as a whole (Table 7.4).

Table 7.4: Breeding success of Shy albatrosses at study and control nests in the North colony, Albatross Island 1995/96 to 1997/98.

Year	Group	No. eggs laid	Hatching success	Fledging success	Overall breeding success
1995/96	Study	5	100%	100%	100%
	Control	222	71%	22%	16%
1996/97	Study	4	100%	75%	75%
	Control	247	74%	68%	51%
1997/98	Study	4	100%	75%	75%
	Control	267	61%	75%	36%

7.3.2 *Chick provisioning*

At Albatross Island, the fledging period of Shy albatrosses is 127 ± 7.4 days (n=10). Chicks received 99 ± 12.4 meals averaging 371 ± 166.6 g (range 40-840 g, n=1,090 meals) after being left alone on the nest, and these totaled 37.3 ± 0.69 kg of food (range 31.7-45.4 kg, n=11; Table 7.5) from the end of brood to fledging. Chicks fasted 22 ± 17.7 hrs between meals (n=1079), and received an average of 1.1 feeds per day. Overall provisioning rates were 386 ± 37.2 g/day (n=11, range 337-450 g/day, Table 7.5).

Chicks were fed almost exclusively during the day, with all but 19 of 1,245 meals (98.5%) delivered between the beginning of nautical twilight in the morning and the end of nautical twilight in the evening. There were no differences between years in the distribution of feeding times (χ^2=42.85, df=46, p=0.605). Of the 1,226 feeds, 82.2% (1,024) were delivered during daylight hours, with 166 (13.3%) and 34 (2.7%) being delivered during the morning and evening twilight periods, respectively. However, chicks were not equally likely to be fed during each daylight hour, with a strong bias towards feeds early in the morning and late in the evening (χ^2=483.17, df=18, $p < 0.001$). This was true for deliveries both by males (Figure 7.3a) and females (Figure 7.3b). While females were slightly more likely than males to deliver meals during the middle of the day, this difference was not statistically significant (paired t-test on proportion of feeds delivered by males and females per hour, t=-1.12, df=23, p=0.137).

Table 7.5: Summary of the provisioning parameters (meal size, fasting interval, total food received, and provisioning rate) from the chicks perspective. Mean data provided at the bottom of the Table includes data only from chicks that fledged. Data were collected from Albatross Island, Tasmania, during three consecutive breeding seasons, 1995/96 to 1997/98.

Nest	Year	Chick age (days)		Food received (g)				Provisioning rate (g/day)		
		start	fledging	# Meals weight/ no weight	Average Meal size (g)	Average Fasting Interval (h)	total food (g)	Overall	To peak mass	Peak mass to fledging
I3	95/96	37	128	94 / 4	357	22	35,430	385	383	394
	96/97	23	115	95 / 1	333	22	31,740	341	344	232
	97/98	27	died at 95 days	62 / 0	303	18	18,760	272	-	-
R45	95/96	34	134	110 / 7	390	20	45,410	450	480	375
	96/97	26	126	106 / 0	408	22	43,260	428	*	*
	97/98	29	126	110 / 0	367	21	40,490	413	416	373
Z7	95/96	28	136	112 / 0	386	22	43,430	398	*	*
	96/97	22	112	102 / 0	331	20	33,790	371	374	96
	97/98	24	133	108 / 0	414	23	44,730	407	426	243
R35	95/96	33	127	85 / 3	370	24	32,832	346	377	262
	96/97	19	died at 113 days	90 / 0	325	24	29,230	308	-	-
Z6	95/96	31	129	94 / 6	367	23	36,230	366	446	182
V5	97/98	37	unknown	72 / 1	316	22	22,890	337	345	226
Mean ± SD				**99 ± 12.4**	**367 ± 31.5**	**22 ± 1.2**	**37,294 ± 6,926.3**	**386 ± 37.2**	**399 ± 46.2**	**265 ± 99.3**

* mass increased to fledging

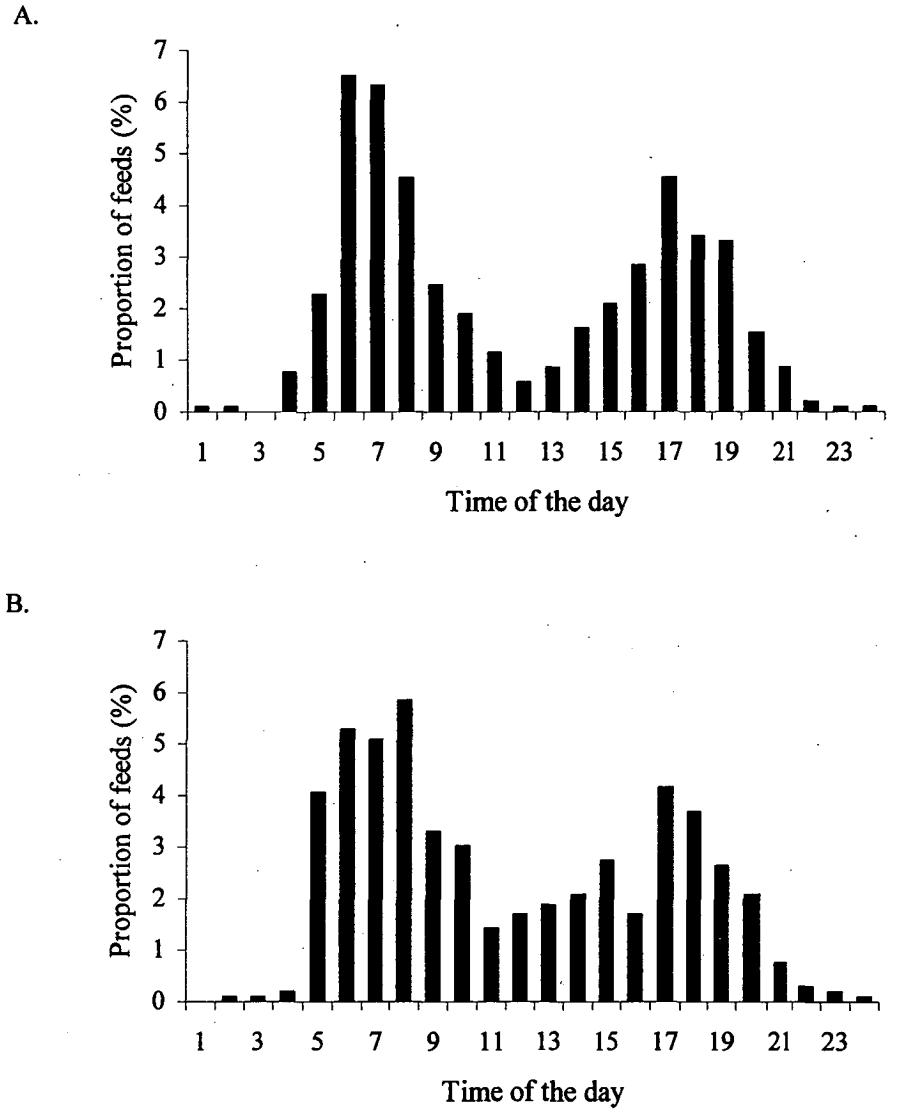


Figure 7.3: Proportion of meals delivered per hour by adult (A) males and (B) females.

7.3.2.1 *Food received by chicks*

7.3.2.1.1 Size of meals received

The sizes of meals delivered to chicks increased with age in each year (Figure 7.4, repeated measures ANOVAs, $F_{8,32}$=8.14, H-F adj $p < 0.0001$, $F_{9,18}$=7.27, H-F adj p= 0.020, $F_{7,14}$=8.32, H-F adj p=0.010, respectively), and in all cases the change through time was linear (polynomial contrasts, $F_{1,4}$=23.58, p= 0.008, $F_{1,2}$=16.30, p=0.056, and $F_{1,2}$=25.31, p=0.037, respectively). Average meal sizes increased from less than 200 g when chicks were 20-29 days old to between 400 and 500 g when chicks were 70 days and older.

Meal size also continued to increase after chicks had reached peak mass (353 ± 30.1 g to 455 ± 63.8 g, n=9 nests; repeated measures ANOVA, $F_{1,8}$=16.74, p=0.003).

The size of meals was similar between years, both at nests studied longitudinally, as well as when all nests were pooled together (Figure 7.4, two-way repeated measures ANOVAs, $F_{2,5}$=1.49, p=0.310, $F_{2,8}$=0.583, p=0.581, respectively). It was also of interest to determine whether the size of the meals delivered to chicks were related to adult foraging trip durations. As meal size increased with chick age (Figure 7.4), a Spearman rank regression analysis was run on adult foraging trip duration against the residuals of the regression of meal size against chick age. Meal sizes were unrelated to adult foraging trip durations (Spearman rank regression, R=0.00, p=0.418).

7.3.2.1.2 Chick fasting intervals

Chicks tended to fast longer between meals as they got older (Figure 7.5), repeated measures ANOVAs, $F_{9,36}$=4.20, H-F adj. p=0.047, and $F_{9,18}$=4.78, H-F adj p=0.002,and $F_{7,14}$=7.33, H-F adj p=0.002, respectively), and in all years the change through time was linear (polynomial contrasts, $F_{1,4}$=13.50, p=0.021, $F_{1,2}$=18.04, p=0.051, $F_{1,2}$=79.36, p=0.012, respectively). Chick fasting intervals increased almost two fold from approximately 14 hours when chicks were 30 days old to 30 hours when chicks were 70 days and older (Figure 7.5). Fasting intervals continued to increase after chicks had reached peak mass (21 ± 1.1 h vs. 36 ± 8.1 h, n=9 nests; repeated measures ANOVA, $F_{1,5}$=20.43, $p < 0.01$).

Chicks fasted for similar durations between meals in each year, both at longitudinally studied nests, and again when all nests were pooled together (Figure 7.5, two-way

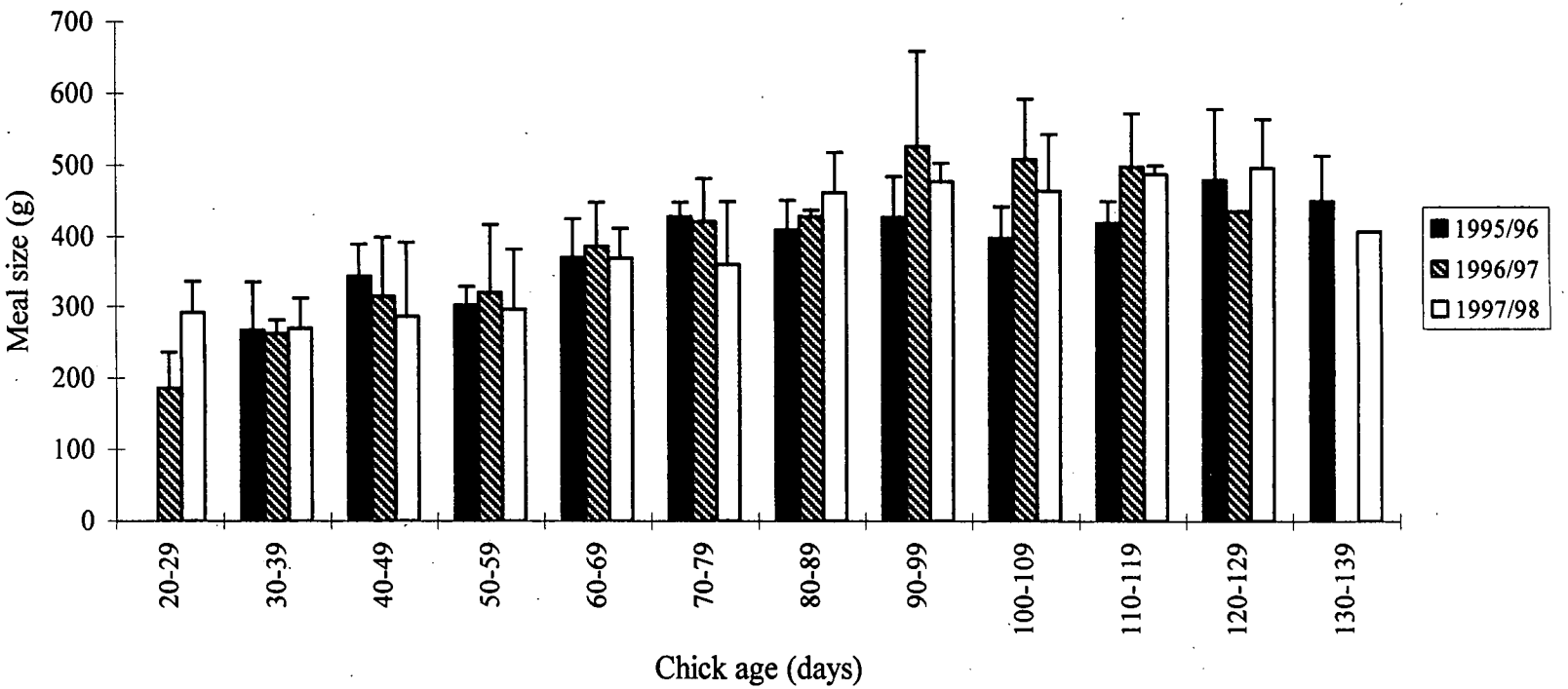


Figure 7.4: Average size of the meals (± SD) delivered to Shy albatross chicks according to age, during the three study years.

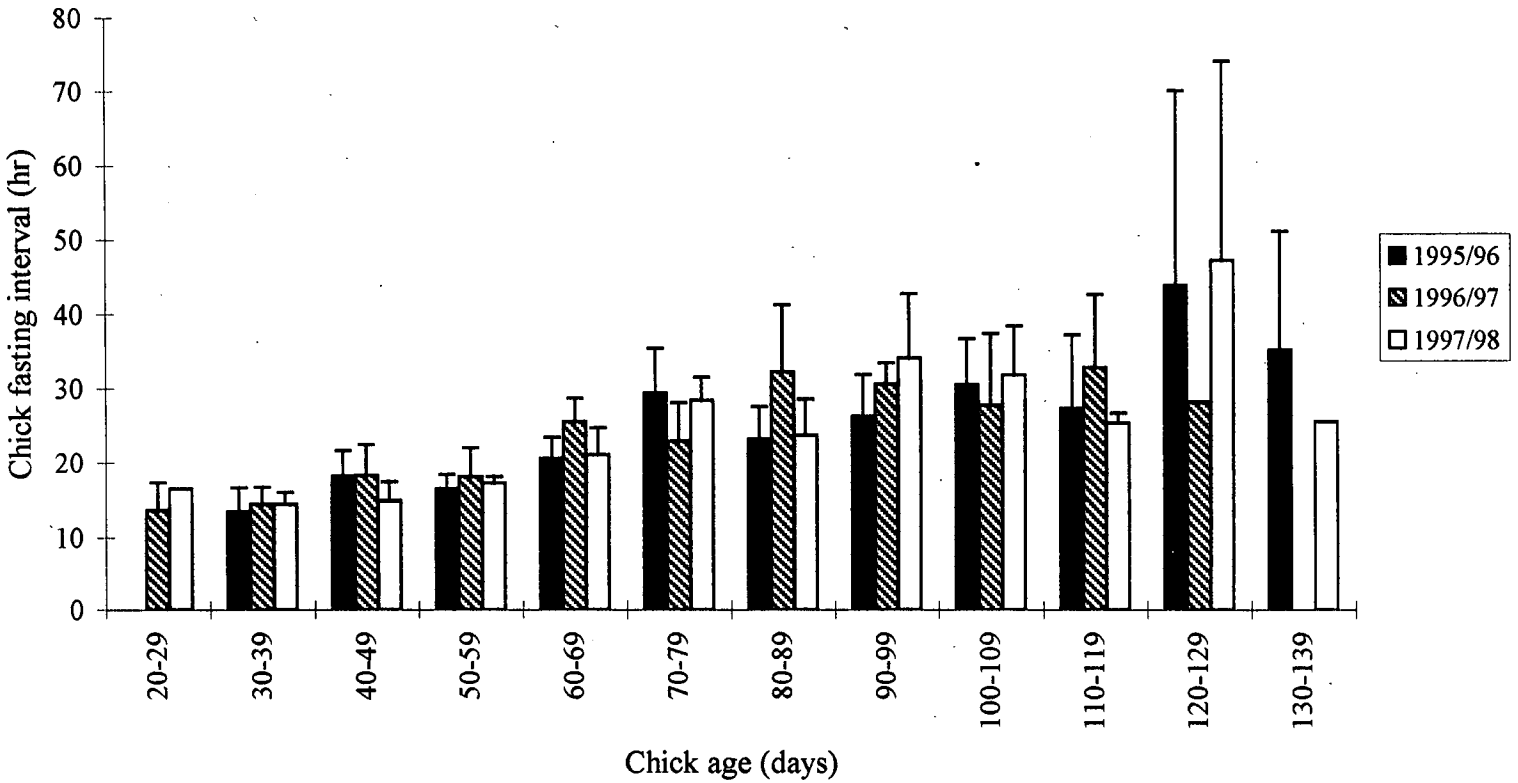


Figure 7.5: Average time between successive meals (± 1 SD) delivered to Shy albatross chicks according to age, during the three study years.

repeated measures ANOVAs, $F_{2,5}$=1.50, p=0.308, and $F_{2,8}$=0.629, p=0.557).

7.3.2.1.3 Chick provisioning rate

The increase in time between meal deliveries was counterbalanced by increased meal size, such that chicks were provisioned at a constant rate (in g/day) from the end of brood/guard until fledging, in all study years (repeated measures ANOVAs, $F_{9,36}$=1.89, H-F adj p=0.085, $F_{9,18}$=1.63, H-F adj p=0.246, $F_{7,14}$=0.180, p=0.840, respectively). Although possibly provisioned slightly less when very young (20-29 days), and again when close to fledging (120-139 days), chicks were provisioned at a steady 300 and 400 g/day in the intervening period (Figure 7.6).

Provisioning rates dropped close to fledging, with chicks receiving 130 g less food per day after they had reached peak mass (398 ± 47.9 g/day vs. 265 ± 99.4 g/day, repeated measures ANOVA, $F_{1,8}$=15.85, p=0.004).

Chick provisioning rates were similar between years, both at nests studied longitudinally, and again when all nests were pooled (Table 7.5, two-way repeated measures ANOVAs, $F_{2,5}$=1.16, p=0.039, and $F_{2,8}$=0.081, p=0.923, respectively).

The amount of food chicks received per day was also examined relative to their body mass (i.e., mass specifically in g/kg$^{0.75}$/day). While the quantity of food delivered to chicks remained relatively steady per day, there was a progressive decrease in the amount of food received per kg$^{0.75}$ per day throughout the rearing period (repeated measures ANOVAs, $F_{9,36}$=8.28, H-F adj p < 0.001, $F_{9,18}$=5.04, H-F adj p=0.003, $F_{7,14}$=6.78, H-F adj p=0.008, for 1995/96, 1996/97 and 1997/98, respectively). The decrease through time was linear (polynomial contrast, $F_{1,4}$=19.88, p=0.011, $F_{1,2}$=38.62, p=0.025, $F_{1,2}$=85.28, p=0.008, respectively). While at the end of the brooding period chicks received approximately 200 g/kg$^{0.75}$/day, at fledging they received less than 100 g/kg$^{0.75}$/day (Figure 7.7).

7.3.2.1.4 Provisioning of male and female chicks

Mean values for the provisioning parameters of known sex chicks are given in Table 7.6. While the sample sizes were very small (three female and four male chicks), and hence there was limited power to detect significant differences, there was some indication that the effort required to fledge a male as opposed to a female chick was different. When standardized for differences in body size (body mass$^{0.75}$), meal sizes and overall mass

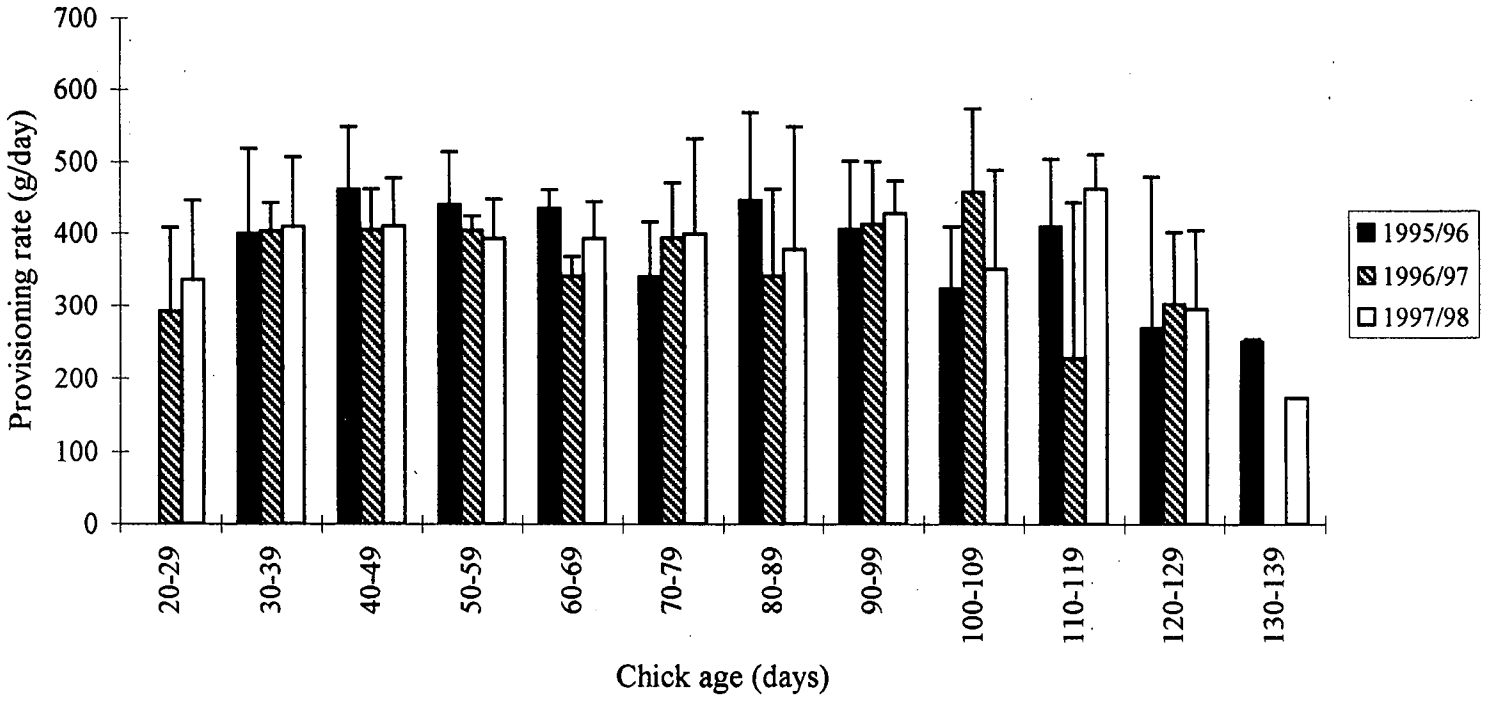


Figure 7.6: Average provisioning rate (± 1 SD) of Shy albatross chicks, according to age, during the three study years.

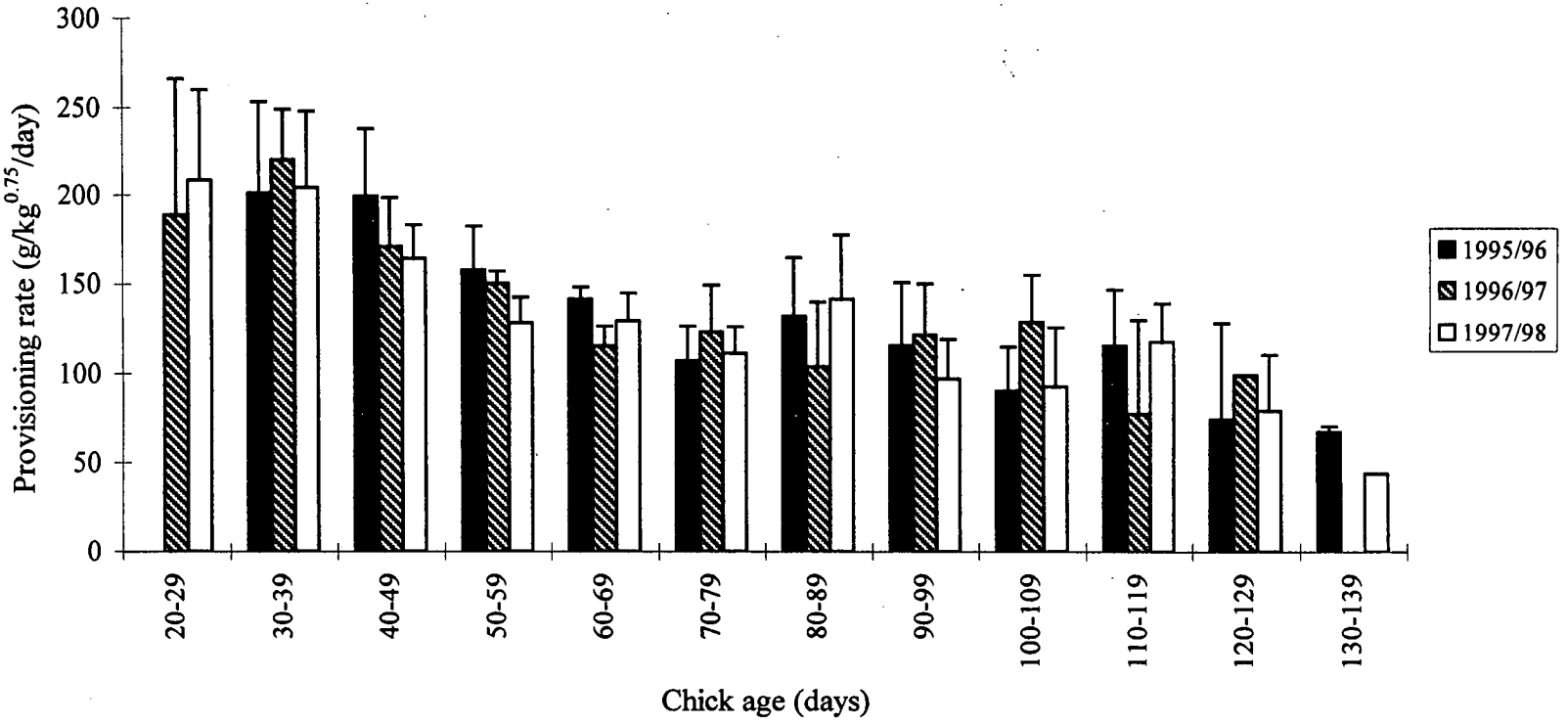


Figure 7.7 Average mass specific provisioning rate (± 1 SD) of Shy albatross chicks, according to age, during the three study years.

specific provisioning rates were similar for male and female chicks (Table 7.6). However, male chicks were provisioned for an average of 10 days longer, and they required almost 22% more total food than females, equating to approximately 10 kg across the fledging period. Therefore, while there are no relative differences in the amount of food required by male and female chicks, because of their larger ultimate body size, male chicks require more food overall. Some sex differences were expected, given that male chicks are both significantly larger and heavier than females at fledging (Hedd et al. 1998, and Chapter 2).

Table 7.6: Mean (± 1 SD) provisioning parameters of the known sex Shy albatross chicks from the end of brood/guard until fledging.

Parameter	Female chicks n=3	Male chicks n=4	t-test, p level
Meal size (g)	345 ± 22.0	376 ± 45.3	t=1.09, p=0.327
Meal size (g/kg$^{0.75}$)	117.3 ± 5.53	128.5 ± 9.47	t=-1.78, p=0.151
Fasting Interval (h)	22 ± 2.0	22 ± 1.0	t=-0.11, p=0.917
Provisioning rate (g/kg$^{0.75}$/day)	120.0 ± 6.97	135.2 ± 11.29	t=-1.99, p=0.117
Fledging period (days)	118 ± 7.9	128 ± 4.0	t=2.01, p=0.115
Estimated food delivered from hatching to fledging (kg)*	37.6 ± 0.22	47.7 ± 0.14	t=-6.89, p=0.002

*See section 7.3.3.3. Excludes chick at V5 (97/98) when automatic nest stopped working prior to fledging

7.3.2.2 *Provisioning parameters at successful and unsuccessful nests*

While similar sized meals were delivered at successful and unsuccessful nests (346 ± 16.0 g vs 334 ± 39.5 g, respectively; two-way ANOVA, $F_{1,11}$=0.149, p=0.707), chicks that died were fed less often (22 ± 0.4 h vs 20 ± 1.3 h, respectively, two-way ANOVA, $F_{1,11}$=7.43, p=0.017). Overall provisioning rates, however, were similar (405 ± 44.4 g/day vs. 360 ± 57.6 g/day, respectively, two-way ANOVA, $F_{1,7}$=1.73, p=0.215). At successful nests the provisioning rate remained relatively constant per day until fledging, while the two chicks that died were provisioned progressively less per day from the time they were 60-69 days old. The male at nest I3 in 1997/98 last fed the chick when it was 71 days old (and then deserted), while the last feed from the female came when the chick was 76 days old. The female next returned to the colony nine days later without delivering any food, and again 20 days after that, but the chick had already died. While it seems clear that this chick starved, the reason for the death of the R35 chick in 1996/97 was less clear. The chick was last fed by the female when it was 74 days old, but was regularly fed by the male until 106 days old. The male next visited the colony six days later, and from the mass records it seems that the chick died either on that or the next day, when it weighed

approximately 4.0 kg. This chick was dissected shortly after it died, and assigned a condition score of 4 (on a scale of 0-5), indicating that it still had substantial fat reserves.

7.3.2.3 *Sex differences in the provisioning performance of adults*

A summary of the provisioning performance of each adult is provided in Table 7.7, along with overall descriptive statistics for male and female parents. As a result of gaps in the data outlined above, analyses of differences in male and female provisioning performance were restricted to periods when chicks were aged between 30-100 days in 1995/96, 20-90 days in 1996/97, and 30-100 days in 1997/98.

Expressed as a difference score for each pair (mean male score - mean female score), gender differences in meal size, feeding interval and overall provisioning rates were constant throughout the rearing period in all years (repeated measures ANOVAs, meal size: $F_{5,20}$=0.99, H-F adj p=0.48, $F_{6,6}$=3.44, G-G adj p=0.08, and $F_{6,12}$=0.57, H-F adj p=0.75; feeding interval: $F_{5,20}$=0.79, H-F adj p=0.570, $F_{5,5}$=0.15, G- G adj p=0.971, and $F_{5,10}$=0.39, H-F adj p=0.575; provisioning rates: $F_{5,20}$=0.17, H-F adj p=0.972, $F_{6,6}$=0.84, G-G adj p=0.528, and $F_{7,14}$=2.31, H-F adj p=0.122, for 1995/96, 1996/97, and 1997/98, respectively). That is, the provisioning patterns of males and females varied in a similar manner through time.

In all years, males and females delivered similar sized meals to their chicks (Table 7.7, one sample t-tests, t=2.60, df=4, p=0.06, t=0.31, df=1, p=0.81, and t=-0.31, p=0.79, respectively), they fed their chicks at similar intervals (one sample t-tests, t=0.54, df=4, p=0.618, t=-0.301, df=1,p=0.814, and t=0.30, df=2, p=0.794, respectively), and overall, they provisioned them at similar rates (one-sample t-tests; t=0.10, df=4, p=0.923, t=0.31, df=4, p=0.810, and t=-0.532, df=2, p=0.648, respectively).

7.3.2.4 *Consistency in the provisioning performance of individual parents through time*

While there were no gender differences in provisioning performance, all parents certainly did not provision their chicks equally well, and this often resulted in large imbalances within pairs (Table 7.7). Furthermore, at all nests with data spanning two or more years, these imbalances and the relative provisioning performance of the birds involved, remained consistent across years (Table 7.7). At two of these nests (R45 and Z7) the female was consistently the better provider, while at the other two nests (I3 and R35), the male consistently provided more food. For example, at nest Z7 the female delivered 66 ±

Table 7.7: Provisioning performance of individual male and female Shy albatrosses from the end of brood/guard until fledging. Summary data at the bottom of the Table include only chicks that fledged. Data were collected at Albatross Island, Tasmania, for three consecutive breeding seasons, 1995/96 to 1997/98.

			Female					Male					Unknown Deliverer	
Nest	Year	Breeding outcome	# Meals weight/ no weight	Average meal size (g)	Average Feeding interval (h)	Total food (g)	Overall provisioning rate (g/day)	# Meals weight/ no weight	Average meal size (g)	Average feeding interval (h)	Total food (g)	Overall provisioning rate (g/day)	# Meals weight/ no weight	Total food (g)
I3	95/96	Fledged	38 / 0	296	50	11,260	122	54 / 4	402	36	23,570	256	2	600
	96/97	Fledged	25 / 0	392	49	4,340	47	62 / 1	392	31	24,450	263	8	2,950
	97/98	died	30 / 0	317	33	9,505	138	30 / 0	286	34	8,585	124	2	670
R45	95/96	Fledged	67 / 2	385	34	26,710	264	43 / 5	400	44	18,700	185	0	0
	96/97	Fledged	99 / 0	421	24	41,690	413	7 / 0	224	25	1,570	15	0	0
	97/98	Fledged	62 / 0	324	36	20,085	205	48 / 0	418	48	20,085	205	1	320
Z7	95/96	Fledged	72 / 0	381	34	27,465	252	40 / 0	399	58	15,965	146	0	0
	96/97	Fledged	58 / 0	351	31	20,375	224	38 / 0	284	51	10,795	114	6	2,620
	97/98	Fledged	72 / 0	459	38	33,060	301	35 / 0	319	64	11,150	101	1	520
R35	95/96	Fledged	29 / 1	309	54	9,635	101	47 / 2	386	37	18,857	199	9	4,340
	96/97	died	27 / 0	237	36	6,410	67	56 / 0	364	35	20,360	214	7	2,460
Z6	95/96	Fledged	51 / 3	333	42	17,710	179	43 / 3	407	34	18,520	187	0	0
V5	97/98	Fledged	31 / 0	284	44	8,810	130	40 / 1	340	40	14,080	207	0	0
Mean			**55**	**358**	**40**	**20,104**	**203**	**42**	**361**	**43**	**16,158**	**171**		
SD			**22.7**	**54.9**	**9.1**	**11,407.5**	**103.7**	**13.8**	**62.0**	**11.8**	**6,553.2**	**72.4**		

7.2% of the total food (range 60-74%) to the pairs chicks across years, whereas at nest I3, the male delivered 72 ± 7.6% (range 66-77%) of the food in the years when this pair was successful.

Defining the poor provider within each pair as the bird delivering the least amount of food, it was clear that poor provisioning performances resulted both from the delivery of smaller meals (322 ± 70.9 g vs. 389 ± 34.2 g, Wilcoxon Matched Pairs, Z=1.95, p=0.050) at less frequent intervals (51 ± 7.2 h vs 35 ± 3.0 h, Wilcoxon Matched Pairs, Z=2.93, p=0.003). There was no indication, at least in this small sample, that parental quality was age related, as the average age of the good and poor quality parents was similar ("good" parents 13.2 ± 2.59 years vs. 13.6 ± 1.14 years for "poor" quality parents, n=5, t=0.316, p=0.380). However, there was little variation in the age of the known age parents, with no birds younger than 10 or older than 16 years in the sample, and this was perhaps limiting.

7.3.2.5 *One parent chicks and regulation of provisioning effort*

In this and a larger study of year-round colony attendance patterns (Chapter 5), single parents were responsible for chick feeding during a portion of the post-brood rearing period at four successful nests. Three of these desertions were by members of pairs also involved in this study; two by males, one at nest Z6 in 1995/96, and the other at nest R45 in 1996/97, and one by the female at nest I3 in 1996/97. The number of visits single parents made to their chicks was compared with one-half the number of visits made by birds feeding within pairs. In 1995/96 numbers were similar (χ^2=1.40, df=1, $p > 0.05$), indicating that at least these single parents did not alter their provisioning schedules. However, in 1996/97, single parents made substantially more than half the number of deliveries that dual parents made to their chicks (χ^2=96.9, df=1, $p < 0.001$), and their overall provisioning rates were also significantly greater (χ^2=299.2, df=1, $p < 0.001$). As these single parents were studied longitudinally, their provisioning performance was also compared in years when they fed alone as opposed to along with their mates. When feeding alone, these parents increased both the number of meals delivered to the chicks (χ^2=16.9, df=2, $p < 0.05$), and their overall provisioning rates (χ^2=135.0, df=1, $p < 0.001$). Differences largely resulted from the increased provisioning performance of the female at nest R45. This bird delivered meals that averaged 20% larger, and her delivery rates were 42% more frequent when she was feeding alone (Table 7.7). While the male at I3 delivered significantly more meals than would have been expected from the

performance of other pairs, this seemed to result from his naturally high provisioning rate (Table 7.7). His performance did not seem to be influenced by the desertion of his mate.

The total amount of food delivered to the R45 chick when fed by a single parent for the entire post-brood provisioning period was substantial (40.49 kg), 3 kg more than the average delivered to chicks during this period (Table 7.5). However, not all chicks fed by single parents fledged. At both nests where chicks died, their deaths were precipitated by variable periods of single parent attendance (see above).

Parents decreased provisioning rates when their chicks were well fed. In 86 instances individual parents were observed to feed their chick twice within a 10 hour period. There was no relationship between the size of these two meals (Spearman rank correlation: young chicks < 50 days, r=0.118, p=0.469, n=40, older chicks ≥ 50 days, r=0.231, p=0.123, n=46), but the second meal was significantly smaller than other meals delivered by that parent within the appropriate 10 day period (287 ± 154.1 g vs. 318 ± 91.6 g, Wilcoxon Matched Pairs test, Z=2.47, p=0.013). The interval to the subsequent meal was also longer, but not significantly so (34 ± 25.6 h vs. 29 ± 11.2 h, Wilcoxon Matched Pairs test, Z=-1.43, p=0.144).

7.3.3 *Chick growth*

Chicks increased in mass from 2.09 ± 0.36 kg (n=11) at the beginning of the study (approximately the end of brood/guard) to 5.02 ± 0.558 kg at fledging (n=10, Table 7.8). Individual chicks reached peak mass (5.50 ± 0.509 kg) between 90 and 130 days of age (109 ± 12.9 days, Table 7.8). Chicks were mostly fed to within days of their departure from the nest (fasting period 2.5 ± 1.58 days, range 1-6 days, n=10), although at a reduced rate (see above), and as a result there was no excessive mass recession prior to fledging (Figure 7.8). Chicks also remained around cliff edges exercising their wings prior to leaving the colony, however the length of time spent there was unknown.

7.3.3.1 *Gompertz Growth Curves*

Individual chick mass and age at the start of the study, at peak mass and again at fledging is provided in Table 7.8, along with the Gompertz parameters describing their growth. The average Asymptotic mass (A) estimated from fitting Gompertz curves was 5.76 ± 0.589 kg and this accorded well with the actual average peak mass of 5.50 ± 0.509 kg (Table 7.8). Growth rate constants (k) ranged from 0.031 to 0.052, and the age at maximum growth or the inflection point (t_i) was reached when chicks were 31 ± 2.81

Table 7.8: Gompertz parameters describing the growth in mass of individual Shy albatross chicks from hatching through to fledging. Gompertz parameter estimates (A, k and t_i) are presented as the mean ± 1 standard error.

Year	Nest	Start		Predicted	Peak mass			Growth	Age at	Fledging			R^2
		Age (days)	Mass (kg)	Asymptotic mass (A) kg	Age (days)	Mass (kg)	Growth (g/day)	constant (k) * 1000	maximum growth (t_i)	Age (days)	Mass (kg)	Growth (g/day)	
1995/96	I3	37	2.36	4.76 ± 0.053	105	4.81	35.5	52 ± 4.3	32 ± 1.23	128	4.41	22.3	0.934
	R35	33	2.40	5.57 ± 0.084	95	5.28	45.7	43 ± 3.4	33 ± 1.02	127	4.66	23.8	0.943
	R45	34	2.67	6.10 ± 0.092	105	5.88	44.6	39 ± 3.02	34 ± 1.13	134	5.29	25.9	0.936
	Z6	31	2.25	5.84 ± 0.086	95	5.91	56.3	48 ± 4.6	28 ± 1.28	129	4.52	22.9	0.896
	Z7	28	1.84	6.09 ± 0.075	135	6.09	39.4	38 ± 2.2	34 ± 0.75	136	5.60	34.5	0.958
1996/97	I3	23	2.08	5.01 ± 0.073	105	4.79	32.7	41 ± 2.5	25 ± 0.75	115	4.61	27.2	0.955
	R45	26	1.71	5.68 ± 0.076	125	5.71	40.0	39 ± 2.2	32 ± 0.69	126	5.35	36.0	0.963
	Z7*	22	1.50	-	105	4.88	40.2	-	-	112	4.41	32.0	-
1997/98	R45	29	1.73	6.09 ± 0.116	115	5.82	47.0	32 ± 2.3	30 ± 0.91	126	5.45	38.0	0.954
	V5	37	2.43	5.58 ± 0.170	95	5.26	48.0	38 ± 4.3	31 ± 1.19	-	-		0.945
	Z7	24	2.07	6.83 ± 0.150	115	6.06	43.4	31 ± 2.4	32 ± 1.08	133	5.92	35.0	0.932
Mean			**2.09**	**5.76**	**109**	**5.50**	**43.0**	**37**	**31**	**127**	**5.02**	**29.4**	-
SD			**0.360**	**0.589**	**12.9**	**0.509**	**6.48**	**13.9**	**2.81**	**7.4**	**0.558**	**6.22**	
All chicks pooled (n=10)													
Mean				**5.93**				**35**	**31**				**0.872**
SD				**0.052**				**1.0**	**0.49**				

* Calibration of this automatic nest post-fledging indicated a failure in the weighing platform in the 4-6 kg range. While it was not possible to calculate growth data for this chick (because it's unknown when the problem commenced), it was possible to adjust peak and fledging masses, as well as extract the relative pieces of data (ie sizes of meals delivered).

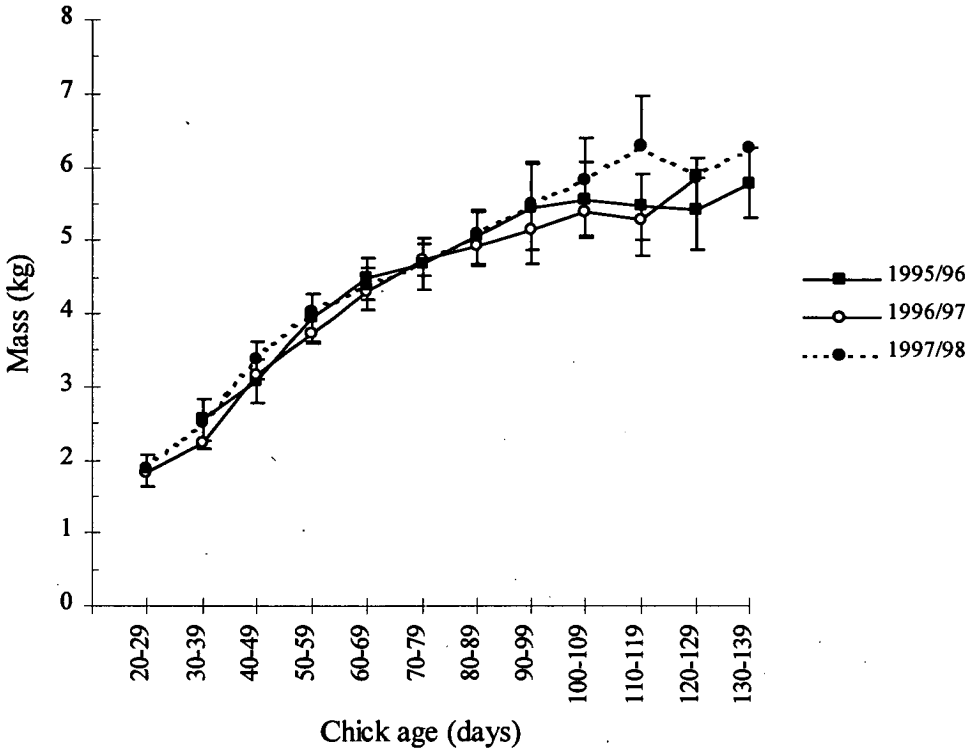


Figure 7.8: Average growth in mass (± 1 SD) of Shy albatross chicks during the three study years.

days old.

Overall growth rates (k) were similar between years (Table 7.8 and Figure 7.8, one-way ANOVA, $F_{2,7}$ =4.06, p=0.068), but with data for just two chicks in 1996/97 and three chicks in 1997/98, sample sizes were small. Unfortunately, calibration of the platform at nest Z7 (in 1996/97) post-fledging indicated that masses were inaccurate by 200-400 g between 4 and 6 kg. As such it was not possible to calculate a growth curve for this chick. Pooling all data allowed a description of the shape of the growth curve for the species, and results are provided in Table 7.8. Asymptotic mass was estimated at 5.93 ± 0.052 kg, and the growth rate constant averaged 0.035 ± 0.001.

There was no obvious difference in the growth rate of the R45 chick in 1996/97 when fed by a single parent (Table 7.8). While this chick grew at 40.0 g/day to peak mass, and this was 3 g/day lower than average, he grew at 36.0 g/day to fledging, a rate 6 g/day above average.

Growth was also described as the time it took for chicks to grow from 10% (t_{10}) to 90% (t_{90}) of asymptotic mass (Table 7.9). t_{10}-t_{90} averaged 80 ± 10.8 days, and during this period chicks gained mass at 58.3 ± 6.58 g/day. This corresponded to an increase of 1.02 ± 0.133% of asymptotic mass per day.

Growth rates from t_{10}-t_{90} and to peak mass were similar for male and female chicks (54.5 ± 2.78 g/day vs. 58.1 ± 6.65 g/day, t=-1.02, df=4, p=0.365, and 44.7 ± 3.78 g/day vs. 39.5 ± 6.53 g/day, t=1.34, df=5, p=0.239), however, from the start of the study to fledging, males grew at a faster rate than females (36.3 ± 1.53 vs. 27.7 ± 4.12, t=3.42, df=4, p=0.027). Male chicks were also heavier at peak mass (5.7 ± 0.34 kg vs. 5.0 ± 0.26 kg, t=3.10, df=5, p=0.027), and at fledging (5.6 ± 0.30 kg vs. 4.6 ± 0.13 kg, t=5.34, df=4, p=0.006). Figure 7.9 shows the average mass of male and female chicks throughout the rearing period. The masses of male and female chicks diverged at approximately 110 days; on average, females lost mass from 110 days to fledging, while the mass of male chicks either remained constant or continued to increase.

7.3.3.2 *Influence of provisioning on chick growth parameters*

Provisioning rates were positively related to chick peak and fledging masses (r^2=0.549, $p < 0.01$, r^2=0.468, $p < 0.05$, Figure 7.10a), with chicks that were provisioned at a higher

Table 7.9: Growth of Shy albatross chicks expressed as the time taken to grow from 10% (t_{10}) to 90% (t_{90}) of asymptotic mass. The absolute mass gain (g/day) during this period is also given, and expressed as the percentage of asymptotic mass gained per day.

Year	Nest	Asymptotic mass		Age		t_{10}-t_{90}	Average daily mass gain	
		kg	% adult mass	t_{10}	t_{90}	(days)	(g)	as % asymptote
	I3	4.76	1.15	3	75	72	52.9	1.11
	R35	5.57	1.35	14	85	71	62.8	1.13
1995/96	R45	6.10	1.47	13	92	79	61.8	1.00
	Z6	5.84	1.41	11	75	64	73.0	1.25
	Z7	6.09	1.47	13	93	80	60.9	1.00
1996/97	I3	5.01	1.21	5	80	75	53.4	1.07
	R45	5.68	1.37	11	90	79	57.5	1.01
	R45	6.09	1.47	5	101	96	50.8	0.83
1997/98	V5	5.58	1.35	9	91	82	54.4	0.97
	Z7	6.83	1.65	6	105	99	55.2	0.81
Mean		**5.76**	**1.39**	**9**	**89**	**80**	**58.3**	**1.02**
SD		**0.589**	**0.142**	**4.0**	**10.1**	**10.8**	**6.58**	**0.133**

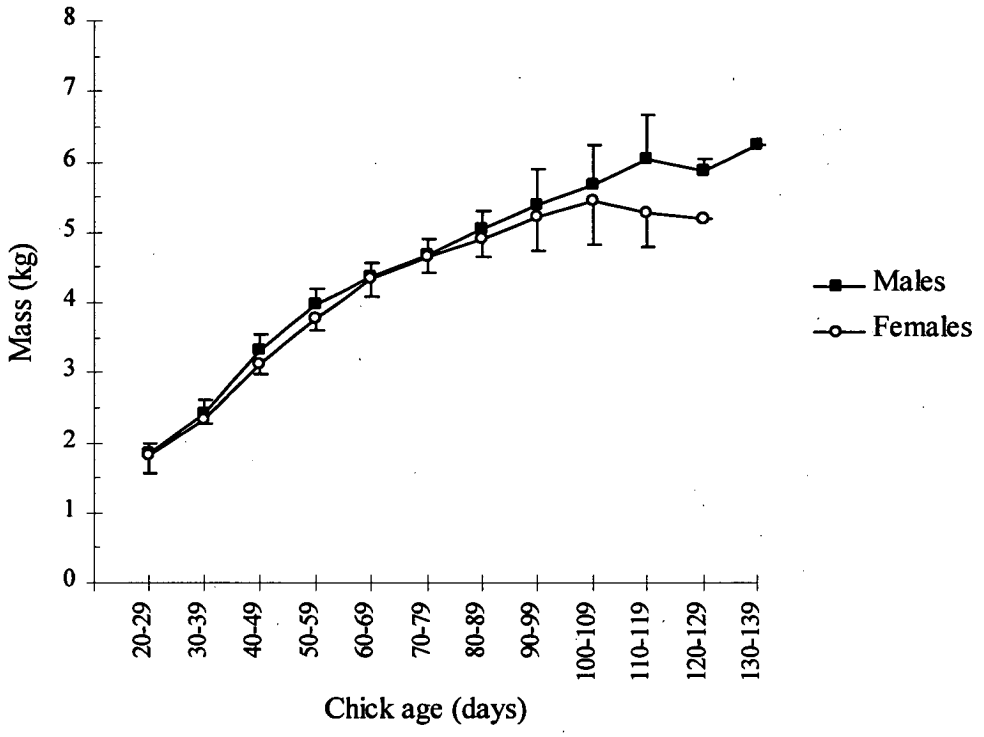


Figure 7.9: Average growth in mass of known sex Shy albatross chicks during the study.

rate per day reaching greater peak and fledging masses. Provisioning rate was also positively related to fledging age (provisioning rate to peak mass r^2=0.448, $p < 0.05$, provisioning rate to fledging, r^2=0.325, p=0.085, Figure 7.10b), with chicks that were provisioned at a higher rate spending longer on the nest. There was, however, no indication that fast growers fledged early or that slow growers fledged late, as the growth rates to both peak and fledging mass were unrelated to fledging age (r^2=0.140, df=9, p=0.287, and r^2=0.027, df=9, p=0.675). This seems to have been driven by the fact that, overall, provisioning rates were unrelated to the absolute growth rates (in g/day) of the chicks (Figures 7.10c and 7.10d).

Stepwise multiple regression analyses failed to enter any of the adult provisioning parameters into equations to predict the growth rates of chicks. Regression of each provisioning parameter against chick growth rates to both peak and fledging mass are given in Figure 7.11. As relationships with overall provisioning rates were presented in Figure 7.10, they are not repeated in Figure 7.11.

7.3.3.3 *Estimates of the total food consumed*

Using the Gompertz growth parameters obtained from pooling all chicks together, the average mass of chicks during each 10 day period from hatching to 39 days was estimated. Then, a fourth order polynomial was fitted to the mass specific provisioning rate data presented in Figure 7.7 in order to estimate the rates for chicks prior to deployment of the automatic nests (from hatching to 29 days of age, broadly, the brooding period). Combining these data, it was possible to estimate the amount of food delivered to the chicks before the automatic nests were deployed, and hence, to estimate the total food consumed from hatching to fledging (Table 7.10). Between hatching and fledging 44.4 ± 0.56 kg of food was delivered to Shy albatross chicks, with a range from 35.6 to 52.7 kg. Known female chicks received 37.6 ± 0.21 kg (n=3) and known male chicks a total of 47.7 ± 0.14 kg (n=3) across the fledging period.

7.4 DISCUSSION

7.4.1 *Chick Provisioning*

Natural variation in the provisioning rates of individual Shy albatrosses were studied

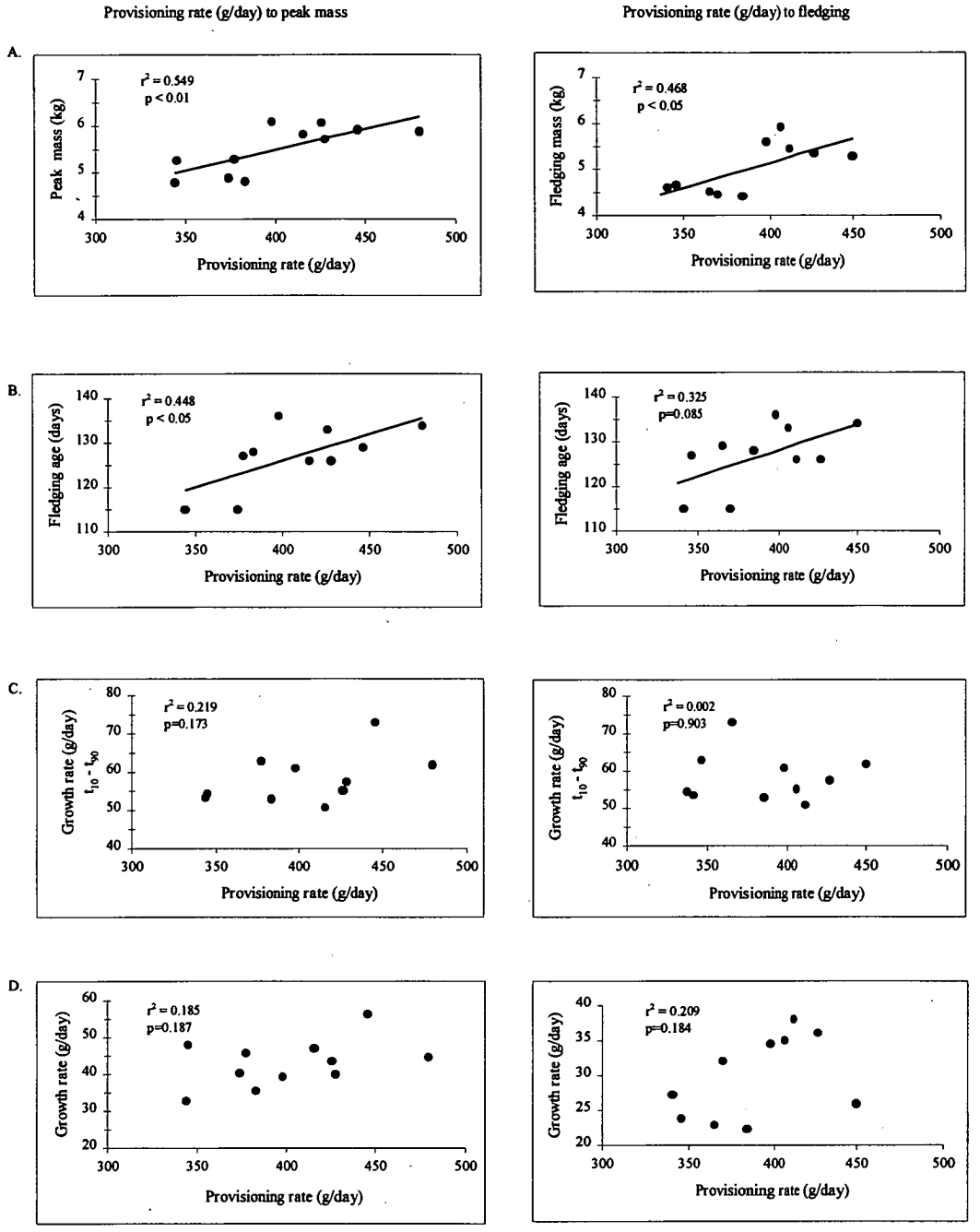


Figure 7.10: Influence of provisioning rate on (A) chick peak and fledging mass, (B) fledging age, (C) the growth rate of chicks from t_{10}-t_{90}, and (D) the overall chick growth rate. Provisioning rates to peak mass are given on the left-hand side of the Figure and provisioning rates through to fledging on the right-hand side.

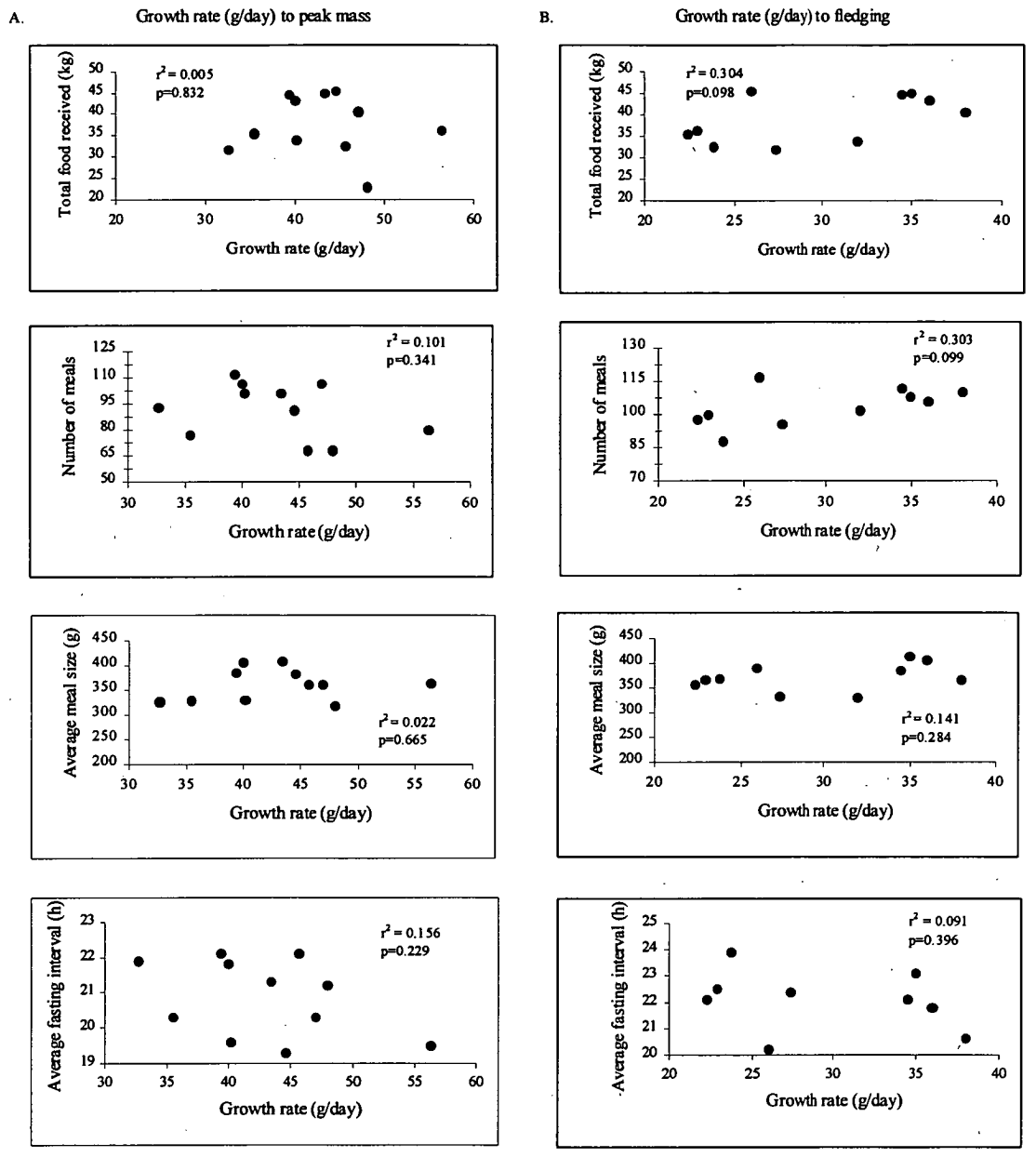


Figure 7.11: Influence of the total food received by chicks, the number of meals delivered, the average meal size and the average fasting interval on chick growth rates to (A) peak mass and (B) to fledging.

during the post-brood chick-rearing period in three successive breeding seasons, 1995/96 to 1997/98. Chicks received meals weighing 367 ± 31.5 g, once every 22 ± 11.2 hours. This translated into each parent delivering a meal approximately once every 40 hours, although there was substantial individual variation. From the end of the brooding period until fledging, chicks were provisioned at 386 ± 37.2 g/day, although this rate decreased somewhat (265 ± 99.3 g/day) after peak mass was reached. It was estimated that from hatching to fledging chicks required 44.4 ± 0.56 kg of food. Although sample sizes were small, there was some indication that male and female chicks required differential provisioning. There were no differences in the relative provisioning rates of male and female chicks, but male chicks were fed for 10 days longer and, overall, they received 22% more food. While there were no sex differences in adult provisioning performance, there were consistent individual differences that most likely related to individual quality. In contrast to the only other known neritic feeding species studied in detail (the Black-browed albatross at Kerguelen Island, Weimerskirch et al. 1997c), some Shy albatrosses have the capacity to increase food delivery rates when their chicks are hungry, and this is accomplished by delivering slightly larger meals at a higher frequency.

Table 7.10: Estimates of the total food consumed by Shy albatross chicks from hatching to fledging.

Nest	Year	Start Age	Estimated food consumed prior to start (g)	Total food consumed start to fledging (g)	Estimated total food consumed (g)
I3	1995/96	37	8,332	35,430	43,762
	1996/97	23	3,830	31,740	35,570
R45	1995/96	34	7,327	45,410	52,737
	1996/97	26	4,755	43,260	48,015
	1997/98	29	5,680	40,490	46,170
Z7	1995/96	28	5,371	43,430	48,801
	1996/97	22	3,522	33,790	37,312
	1997/98	24	4,138	44,730	48,868
R35	1995/96	33	6,992	32,832	39,824
Z6	1996/97	31	6,323	36,230	42,553
				Mean ± SD	**44,361 ± 5557.7**

Despite large scale variation in breeding success in the study colony as a whole, at the study nests there were no inter-annual differences in any of the provisioning parameters. A number of factors could account for this. First, despite the detail of the information collected, in all years the sample sizes were small. Second, while studying the same pairs of birds from one year to the next provided some form of statistical control, the finding

that individuals tended to behave consistently from one year to the next may have introduced bias of its own. In two of the four longitudinally studied nests, parents fledged their chicks in all three years, indicating that these adults were of high quality. It may be that such individuals are capable of maintaining relatively consistent provisioning effort even in years which differ vastly in terms of food availability, a situation reported for Grey-headed albatrosses by Cobley et al. (1998). Related to this, as only successful nests were examined across years there may have again been a bias towards inclusion of high quality parents. As Williams & Croxall (1990) point out, the timing of chick mortality may differ in good and poor years, with only chicks from high quality parents (i.e., heavy chicks) surviving to fledging age in poorer years. Finally, a lethal avian pox virus is prevalent on Albatross Island, being transmitted through fleas and ticks. The effect of the virus and its toll on chick mortality is more pronounced in some years than others. The result is that the virus potentially dissociates any relationship between food availability and breeding productivity at this site. That is, the number of young surviving to fledging age may have little to do with their parents ability to provide them with adequate food. This fact is abundantly clear upon dissection of chick carcasses, as the majority of chicks have substantial fat reserves (condition scores of 3 and above). It appears that in most cases death is caused not by inadequate provisioning, but rather through kidney and liver failure precipitated by the virus (Gales 1993).

During post-brood chick-rearing in 1996/97, birds were foraging over the continental shelf, west-southwest from Albatross Island, at a distance of approximately 120 km (Chapter 8). Foraging at this range would have easily allowed birds to locate prey and return to feed their chicks almost daily. The two birds satellite tracked during this stage showed a high degree of foraging zone consistency, repeatedly returning to the same patch of water to feed. Because of unacceptable implications of disturbance (ie, nest desertions) satellite tracking was only conducted during this part of chick-rearing in one season. Tracking at other times of the year (during incubation and chick-brooding), has confirmed the consistency in foraging zone use at both the individual bird and population levels between years (Chapter 8).

While most meals were delivered during daylight, they were most common either early in the morning or late in the evening. Adults fly and are active on the surface of the water during both the day and night (Chapter 8). Birds also raft off the colonies, but this behaviour is most prevalent during incubation and chick-brooding (personal obs.). Chick feeds early in the morning result either from birds that have been travelling and/or feeding at night and arrive in the colony at dawn or from birds which returned to the

vicinity of the colony the previous evening and have just come ashore to feed. Nocturnal feeds were rare in Shy albatrosses, as also appears to be the case for Black-browed albatrosses (Weimerskirch et al. 1997c). Evening peaks in food delivery could result from prey freshly caught and returned to the chick the same day. The timing of feeds may also indicate the nature of the prey taken. Meals fed to Shy albatross chicks are mostly composed of fresh or partially intact fish (84 ± 6.3% by fresh mass, Chapter 6), predominantly Jack mackerel *Trachurus declivis* and Redbait *Emmelichthys nitidus*. Jack mackerel is an abundant neritic pelagic fish that occurs throughout the coastal waters of southern Australia (Williams & Pullen 1993). Jack mackerel schools in summer and autumn off Tasmania, schools forming just after daylight and again in the hours just before dark to feed on surface swarming krill *Nyctiphanes australis* (Williams & Pullen 1993). Redbait schools with Jack mackerel (Williams & Pullen 1993), and is probably taken by the albatrosses at that time. The albatrosses also prey upon Gould's squid *Nototdarus gouldi* when rearing chicks and this is reportedly the most common cephalopod in the region (C.C. Lu unpubl. data, cited in Gales et al. 1993). The estimated mantle length of some Gould's squid indicated that they were mature individuals, and as they are believed to be semelparous (C.C. Lu unpubl. data, cited in Gales et al.1993), they could have been taken dead at the surface. However, at least 50% of the measurable squids were immature, and could have been taken live at the surface.

While chicks were provisioned slightly less after reaching peak mass, provisioning rates were in the order of 400 g/day until that time. Consistent provisioning rates were maintained despite larger meals being delivered to older chicks, because they were delivered less often (Figures 7.4-7.6). This may be an effort by the adults to reduce foraging costs, as it would be more energetically efficient for adults to deliver larger meals to chicks less often. This change may also indicate that adults are adjusting provisioning schedules according to the size of their chicks or, alternatively, that as chicks grow their larger stomach capacity enables them to accept more of the food brought ashore.

7.4.1.1 *Regulation of provisioning effort & the behaviour of single parents*

Pairs of Shy albatrosses do not appear to provision their chick independently, a finding that contrasts with most other studies of Procellariiforme provisioning behaviour. This, however, can perhaps be explained methodologically. Previous studies reporting independence of chick feeding by the members of a breeding pair were based upon repeated chick weighings with no information on the behaviour of individual parents.

There was, therefore, an implicit assumption in these studies that the members of a breeding pair provisioned their chick equally well, a finding certainly not supported by this study (Table 7.5), or by Weimerskirch et al. (1997b) with Wandering albatrosses. While within-pair differences in this study related to consistent individual differences, and in Wandering albatrosses to sex-specific differences, the critical point is that the contribution of each parent is often not one-half of the whole. We are not advocating that parents consciously co-ordinate their efforts, but it seems plausible that adults respond to one another indirectly through the soliciting behaviour of their chick.

One of the most interesting findings of this study was the individual consistency in provisioning effort from one year to the next. Parents tended to be consistently good or consistently poor providers. The female at nest R45, for example, who was consistently a good provider, was also able to substantially alter food delivery patterns according to the needs of her chick. She provided 59% of the food in 1995/96 (26.7 vs. 18.7 kg), and 50% in 1997/98 (20.1 kg each), while in 1996/97, following desertion of her mate, she almost doubled her average provisioning effort, and provided 41.7 kg of food to the chick. During 1996/97 her meals were 19% larger than in previous years, but perhaps more significantly, these meals were delivered more often. Her chick feeding interval decreased by 46%, from an average of 35 hours when feeding with her mate, to just 24 hours when she fed the chick alone. This response must have been mediated by the behaviour of the chick, either actively, through increased begging intensity, or more passively, as suggested by Weimerskirch et al. (1997c), by simply swallowing all the food delivered. Irregardless of the mechanism, the chick somehow conveyed its nutritional status and this bird was able to respond by decreasing the interval between meals.

Single parents, however, were not always able to increase provisioning rates when their chicks were hungry, and the behaviour of some parents was unaltered by desertion of their mate. Parents do seem able to detect chick nutritional status, but if they cannot increase their foraging efficiency or they are not willing to expend more energy, they may be unable to respond. However, both the increase in provisioning effort by the R45 female in 1996/97 and the ability of birds to decrease provisioning effort when chicks are well fed, seem to be true behavioural responses of adults to requirements of chicks. Black-browed albatrosses similarly decreased provisioning rates when chicks were experimentally overfed (Weimerskirch et al. 1997c). However, that just one of the three single feeding Shy albatrosses in this study was able to increase provisioning effort indicates that it may not be a behavioural option open to all birds. This bird was 14 years

old in 1995/96, and she was known to have breed successfully on at least one occasion in the past. As Shy albatrosses begin breeding as young as 5 years (N. Brothers, unpubl. data), this bird could possibly have had 9 years previous breeding experience. While in this study age appeared to have no effect on breeding success, the age span of the known aged breeders (10 to 16 years) was limiting. It is possible that if age did influence parental quality that its effects might be most obvious in young and inexperienced birds or in older senescent birds (Lequette & Weimerskirch 1990, Weimerskirch 1992). However, individual quality is being increasingly acknowledged as important to breeding and provisioning performance (Becker 1998, Cobley et al. 1998).

Some authors have suggested that the provisioning rate of chicks is limited by the chicks assimilatory capacity (Hamer & Hill 1994, Weimerskirch et al. 1997c). Weimerskirch et al. (1997c) concluded that this may be the case in good years for Black-browed albatrosses breeding at Kerguelen Island when adults tend to deliver larger meals. A negative relationship between the size of two meals delivered within six hours was interpreted to indicate that chicks could not swallow all the food delivered. For Shy albatrosses there was no relationship between the size of two meals delivered within a short period of time (10 hours). However, at comparable ages (35-65 days) Shy albatross chicks are fed much smaller meals (Shy albatrosses 296 ± 148.1 g (40-730) n=475 vs. 534 ± 265 g (100-1300) n=290 for Black-browed albatross chicks in 1994 and 449 ± 216 g (100-1100) n=245 in 1995). The disparity in these meal sizes is even more pronounced when size differences between the species are considered, as Shy albatrosses are 20-30% larger than Black-browed albatrosses. Therefore, it is not apparent that the chicks assimilatory capacity is regulating provisioning rates in Shy albatrosses, at least not in the ages examined. However, when chicks were young (30-40 days) adults were observed to deliver multiple meals during extended visits to the Island. In these instances adults fed the chick soon after arriving and again some hours later, prior to departing the colony. This situation was never observed when chicks were older, perhaps indicating that as chicks grew they could accept all the food parents had to offer.

7.4.1.2 *Comparison with other species*

This study contributes to a growing body of literature indicating that some species of Procellariiformes are able to detect and respond to the nutritional condition of their chicks (Bolton 1995, Weimerskirch et al. 1995, Hamer & Thompson 1997, Weimerskirch et al. 1997c, Weimerskirch 1998c). Weimerskirch et al. (1995, 1997c) and Weimerskirch (1998c) took an experimental approach, manipulating either the foraging efficiency of

adults, or increasing or decreasing food demands at the nest, while the remainder of the studies (this one included), examined natural variation in the rates of food delivery to chicks. While it has been proposed that pelagic species should have greater scope for regulating provisioning effort, in particular, increasing provisioning rates to hungry chicks (Weimerskirch et al. 1995, 1997c), we have found that some Shy albatrosses also have this capacity. This ability contrasts with that for the only other known neritic feeding species to have been studied in detail; the Black-browed albatross at Kerguelen Island (Weimerskirch et al. 1997c).

Despite foraging in a neritic environment, the different regulation capacities of Shy and Black-browed albatrosses may ultimately relate to differences in their foraging strategies. Individual Shy albatrosses repeatedly concentrate foraging efforts over specific patches of water (Chapter 8). While precise locations within these areas may not be revisited on successive trips, birds generally maintain a constant heading from the breeding colony and consequently re-work the same broad patches of water from one trip to the next. This perhaps indicates that while prey are generally widely available and/or distributed over the continental shelf, their distribution is patchy. Black-browed albatrosses in contrast repeatedly commute to specific areas along the Kerguelen Island shelf break, which coincides with a northeast meandering of the Antarctic Polar Frontal Zone (Weimerskirch 1998b). Birds fly quickly and directly to this area, and spend much of their time there, presumably searching for food, before returning to the colony. Shy albatrosses do not forage in this manner. Shy albatrosses forage in inner continental shelf waters, only occasionally frequenting the shelf break, and they also travel much more slowly than reports for other albatross species (Weimerskirch et al. 1993, Weimerskirch & Robertson 1994, Prince et al. 1998). While lower flight speeds may relate to less extreme weather conditions experienced at their breeding locality, it also likely reflects the species foraging strategy. It seems that prey may be encountered at any point along a foraging route, and the lower flight speeds of Shy albatrosses could be seen as adaptive, with birds continually searching for food while at sea. While the 2-3 day foraging trips of Black-browed albatrosses are thought to be as short and efficient as possible, with birds spending one day commuting to and from the foraging grounds, and the remainder searching for food (Weimerskirch et al. 1997c), Shy albatrosses appear not to be similarly constrained. Their provisioning strategy may therefore be relatively more flexible and/or more opportunistic.

Differential availability and distribution of prey, which must drive differences in the foraging strategies of Shy albatrosses and Black-browed albatrosses, are also indicated by

different responses to increased food availability and increased demands at the nest, respectively. In years when food was abundant, Black-browed albatrosses responded not by decreasing the duration of foraging trips but by delivering larger meals to their chicks, suggesting that for this species the duration of foraging trips may already be as short as possible (Weimerskirch et al. 1997c). In contrast, Shy albatrosses increased provisioning rates by slightly increasing the size of the meals delivered, but more importantly, they halved the duration of their foraging trips.

Similar provisioning rates by male and female Shy albatrosses contrasts with the situation described for Wandering albatrosses (Tickell 1968, Weimerskirch et al. 1997b). While both male and female Wandering albatrosses undertake short and long foraging trips when raising chicks, the short trips of females are longer, females spend more time in long trips, and on such trips they gain less mass than males (Weimerskirch et al. 1997b). At South Georgia, Tickell (1968) also noted that males appeared to assume a greater share of the chick feeding near the end of the rearing period. Taken together, such differences indicate differential foraging costs for the sexes, and this can perhaps explain differential parental investment. Male and female Wandering albatrosses have separate foraging areas during the chick-rearing period, and they have also been reported to feed chicks different types of prey (Weimerskirch et al. 1993, 1997b). There is no indication of a separation of the foraging zones for male and female Shy albatrosses (Chapter 8), and as at some nest females were responsible for delivering upwards of 70% of the food to the chick, there is also no indication of a sex difference in foraging costs.

7.4.1.3 *Differential cost of raising male and female chicks?*

Despite small sample sizes, there was some indication that male and female chicks were differentially provisioned. Male chicks are larger and heavier at peak mass and at fledging than females (Hedd et al. 1998, and Chapter 2), and at least in the sample of chicks examined here, they were fed slightly larger meals for an additional 10 days. In combination, this resulted in male chicks receiving an estimated 22% more food than females from hatching to fledging. If typical for the species, this indicates differential costs of raising male and female offspring, with a wide variety of energetic implications. For example, sex-specific chick mortality rates might be expected, especially in years of poor food availability, and for adults energetic costs could be cumulative if, for example, male chicks were raised in a number of successive years.

Differential provisioning of male and female chicks has also recently been found by Weimerskirch (pers. comm.) for Wandering albatrosses. Female chicks received less

total food, they reached a lower peak and fledging mass, and similar to the situation for Shy albatrosses, female Wandering albatross chicks spent a shorter period on the nest (Weimerskirch pers. comm.). The degree of disparity in provisioning effort may be expected to relate to the extent of sexual dimorphism. At fledging, the mass dimorphism index for Shy albatrosses is 92%, while it ranges between 93-97% for their other morphometric measures (Hedd et al. 1998, and Chapter 2). These indices are similar to levels for other black-backed, and great, albatrosses (Marchant & Higgins 1990).

The mechanism driving the extended provisioning period of male chicks is unknown. It may in fact be that the fledging date is primarily determined by the chick, and not it's parents. If so, it could simply be that male chicks demand food for a longer period than females.

7.4.2 *Chick growth*

While growth rates are to some extent species specific in birds (e.g. Prince & Ricketts 1981), the availability of food during chick rearing is also known to be influential, with inter-annual differences in the duration of the fledging period, peak and fledging mass, and overall growth rates described for some species (Barrett & Rikardsen 1992, Weimerskirch et al. 1997c, Cobley et al. 1998, Prince et al. submitted). Age and previous breeding experience are also known to influence the rate of chick growth in Wandering albatrosses, but, at least for this species such influences appear to be limited to the first breeding attempt (Lequette & Weimerskirch 1990).

Shy albatrosses grow at an average rate of 43 ± 6.5 g/day from the end of the brooding period until reaching a peak mass 139 ± 14.2% of adult body mass when they are about 110 days old. Within related species, it is generally the case that larger species grow more slowly than smaller species (Pennycuick et al. 1984). When expressed as a proportion of the asymptotic mass gained per day (to account for species differences in body size, across the period from t_{10} - t_{90}), Shy albatrosses grow more slowly than the smaller Black-browed, Grey-headed and Yellow-nosed albatrosses, but considerably faster than the larger, great albatrosses (Wandering and Royal *Diomedea epomophora*) (Table 7.11). Such differences would be expected on the basis of body size.

Within similarly sized species, however, relative growth rates might also be expected to relate to the pattern of food delivery. Black-browed and Grey-headed albatross chicks receive similar sized meals, they fast for similar durations, and they are provisioned at almost identical rates (542 and 539 g/day to 100 days, Prince et al. submitted). However,

these species have different growth rates (Prince 1980, Ricketts & Prince 1981, Prince et al. submitted), substantially different fledging periods (116 vs. 141 days, respectively), and while Black-browed albatrosses breed annually, Grey-headed albatrosses are biennial breeders (Tickell & Pinder 1975, Prince 1980, Prince et al. submitted). Variation in the quality of the diet is reported to account for these differences, as Black-browed albatrosses feed their chicks mainly krill and fish, which is more energy dense than the squid and fish diet of Grey-headed albatrosses (Clarke & Prince 1980, Prince 1980, Reid et al. 1996).

Shy albatrosses feed their chicks smaller meals more frequently than either Black-browed or Grey-headed albatrosses (Tickell & Pinder 1975, Prince 1980, Weimerskirch et al. 1997c, Prince et al. submitted, Table 7.11), but overall chicks are provisioned at a lower rate, approximately 400 g/day. Being both larger than Black-browed and Grey-headed albatrosses and having a lower provisioning rate, then, it is interesting that the fledging period of this species is an intermediate 127 days. Combining provisioning rates (to 100 days) with overall dietary composition (which averages 28.4%, 46.3%, 25.0%, and 11.7%, 36.0%, 52.3% for krill, fish and squid in Black-browed and Grey-headed albatrosses, respectively, Prince 1980, Reid et al. 1996), and energy content data (4.6, 8.9, and 3.47 kJ/g, respectively, for krill, fish and squid, Clarke & Prince 1980, Croxall & Prince 1982, Cherel & Ridoux 1992), results in energy provisioning rates of 3409 kJ/day and 2989 kJ/day for Black-browed and Grey-headed albatrosses, respectively. A comparable analysis for Shy albatrosses, using the following calorific values (Jack mackerel, 7.54 ± 1.37 kJ/g, for fish; Gould's squid, 5.39 ± 0.30 kJ/g, for cephalopods; and assuming the *Nyctiphanes australis* value of 3.49 kJ/g for both crustaceans and tunicates, Green et al. unpubl. data) results in an average energy provisioning rate of 2821 kJ/day to peak mass.

Regressing the energy provisioning rate against the duration of the fledging period using data from Black-browed and Grey-headed albatrosses, results in an estimated fledging period of 151 days for Shy albatrosses, 24 days in excess of actual. This overestimate likely results from differences in the manner in which these species provision their chicks after they reach peak mass. While the provisioning rate of Shy albatrosses decreases from approximately 400 g/day to 265 g/day after chicks have reached peak mass, this decrease is apparently insufficient, or not sustained for long enough period for the chicks to lose mass. Indeed, the mass of some Shy albatross chicks increased until fledging. Provisioning rates of Black-browed and Grey-headed albatrosses decrease significantly after 100 days (Prince et al. submitted), and while the magnitude of the decrease was not

Table 7.11: Comparative growth and breeding parameters of albatrosses.

Species	Asymptotic mass (kg)	Fledging period (days)	Feeding interval (days)	Growth constant (k)	t_{10}-t_{90} (days)	Mean daily mass gain (g)	as % asymptote	Source
Wandering	11.50	278	-	0.026	164	56.0	0.49	Tickell 1968, Croxall 1990
Royal	10.90	-	-	-	105	83.0	0.76	Richdale 1952
Shy	5.76	127	0.92	0.037	80	58.3	1.02	This study
Black-browed	5.00	116	1.22	0.048	57	70.0	1.40	Ricketts & Prince 1981 Tickell & Pinder 1975 Prince et al. submitted
Grey-headed	4.70	141	1.26	0.042	60	63.0	1.33	Ricketts & Prince 1981 Tickell & Pinder 1975 Prince et al submitted
Yellow-nosed	3.46	115	-	-	54	50.0	1.45	Weimerskirch et al. 1986 Jouventin et al. 1983
Light-mantled sooty	3.45	141	-	0.043	62	45.0	1.30	Thomas et al. 1983
Sooty	3.00	164	-	-	69	37.0	1.23	Weimerskirch et al. 1986

indicated, it was substantial enough to cause considerable mass recession prior to fledgling. It seems, therefore, that species differences in provisioning regimes after peak mass can account for the discrepancy in predicting the duration of the fledging period for Shy albatrosses.

7.4.2.1 *Adult provisioning and chick growth rates*

The rate at which Shy albatross chicks were provisioned positively influenced their peak and fledging masses. However, despite the level of information detail collected on adult provisioning performance, no relationship was found between provisioning rate and the absolute growth rate of chicks (g/day). While the small sample size in this study may have been limiting, subtleties in the manner in which Black-browed and Grey-headed albatrosses were provisioned (meal sizes, fasting intervals, etc.) were also not strongly related to chick growth rates (J. Croxall, pers. comm.). In these species, the overall provisioning rates were, however, related to the absolute chick growth rates (Prince et al. submitted). The relationship for Grey headed albatrosses, however, appeared to be driven by low chick growth rates in 1994, a year noted for poor food availability. Perhaps, then, similar to this study, in years when food was more readily available, chick provisioning and growth rates were less strongly related. While extrinsic factors such as individual chick differences in activity levels or metabolic rates could potentially uncouple provisioning and growth rates, the lack of strong relationships in all three albatross species rather suggests methodological origins. Despite the precision with which information on meal size, feeding frequency and overall provisioning rates were collected, little was known of the composition of the meals, or how their composition changed through time. Evidently along with the effects of the sheer quantity of food and its delivery rate, the composition of the meals must also influence chick growth rates.

Also, similar to one of the caveats placed upon the lack of inter-annual variation in provisioning and growth rates, it could be that relationships between these parameters were not obvious because we were examining the provisioning behaviour of older, experienced birds. Previous experience may act as a buffer against potentially fluctuating resource availability. In the case of Shy albatrosses, at least, breeding in a less seasonal environment may result in food being more or less comparably available in most years. Despite, then, what appeared to be large differences in the provisioning rates, we may have simply been seeing a gradation within "well fed" and the magnitude of these differences may have been insufficient to cause predictable variation in chick growth rates.

7.5 CONCLUSIONS

Being intricately linked with the foraging strategy, and the abundance, availability and predictability of prey within the foraging zones, there can be no single mechanism regulating provisioning behaviour in Procellariiforme seabirds. Indeed, such mechanisms and capacities are likely not even species-specific, given their reliance on prey characteristics. Shy albatrosses forage exclusively in neritic waters close to their colonies, and they feed their chicks small meals relatively frequently. Yet in contrast to predictions regarding the provisioning capacities of neritic and pelagic species (Weimerskirch et al. 1995, 1997c), Shy albatrosses are able to respond to hungry chicks by increasing their provisioning rates. This capacity appears to be linked with individual quality but, overall, it suggests that Shy albatrosses are not delivering food to chicks at a maximal rate. Provisioning effort was often imbalanced within breeding pairs, and longitudinal studies indicated that the relative provisioning performance of individual parents was consistent through time. Given the current focus on species that either breed or feed within the Antarctic or sub-Antarctic, there are potentially a wide variety of undescribed foraging and provisioning strategies employed by tropical and temperate species. Detailed studies, not only of the provisioning behaviour of individual Procellariiforme parents, but also of the nature of their foraging behaviour at sea, are required to elucidate mechanisms regulating provisioning behaviour across the Order, and indeed within seabirds in general.

Chapter 8

FORAGING STRATEGY OF SHY ALBATROSSES *Thalassarche cauta* IN AUSTRALIA: INDICATIONS OF POPULATION-SPECIFIC IMPACTS FROM LONGLINE FISHERIES

8.1 INTRODUCTION

Where there are adequate data to determine albatross population trends, almost half are declining, and by-catch associated with longline fisheries has been implicated in all these declines (Weimerskirch et al. 1997a, Croxall et al. 1998, Gales 1998, Weimerskirch & Jouventin 1998). This realization has stimulated considerable research into the distribution of albatrosses at sea.

The degree to which albatrosses overlap spatially and temporally with longline fisheries provides an index of the actual and potential threats they face. Therefore, when different albatross populations or different age classes use distinct foraging grounds at sea, contemporaneous changes in their population parameters would not necessarily be expected. For example, in recent years divergent population trends have been observed for Wandering albatrosses *Diomedea exulans* breeding on South Georgia in the South Atlantic and at Crozet and Kerguelen Islands in the Southern Indian Ocean. Following intensive longline fishing and concomitant population declines in the 1970's and 1980's, movement of the Japanese Southern Bluefin tuna *Thunnus maccoyii* fishery outside the foraging zones of Wandering albatrosses at the Crozet Islands has allowed recent increase in their population size (Weimerskirch & Jouventin 1998). At South Georgia, however, Wandering albatross populations continue to decline. Despite movement of the Japanese fishery, the downward trends are believed to be maintained by the development of new longline fisheries (for Swordfish *Xiphius gladius*, Hake *Merluccius hubbsi*, Kingclip *Genypterus blacodes*, Patagonian toothfish *Dissostichus eleginoides* and other *Thunnus* species) operating along the South American continental shelf, in areas heavily utilized by birds during the breeding season (Croxall et al. 1998, Prince et al. 1998). Interactions with longline fisheries throughout the Southern Ocean are also believed responsible for population declines of the smaller *Thalassarche*, *Diomedea* and *Phoebetria* albatrosses at all sites (Croxall et al. 1998, Prince et al. 1998, Weimerskirch & Jouventin 1998).

The use of satellite transmitters since the late 1980's has greatly enhanced our knowledge, to the extent that for some of the more well studied populations, a great deal is known of the foraging strategy during the breeding season (Weimerskirch et al. 1993,

Prince et al. 1998, Weimerskirch 1998b). However, information on the distribution of non-breeding birds (adults and juveniles) is lacking for almost all species. Describing the manner in which albatrosses structured their foraging trips during the breeding season, Weimerskirch (1998b) proposed two broad strategies; "commuting", where birds fly rapidly and directly to specific marine localities where much of their time is spent prior to returning to the nest, and "searching", where birds move almost continuously along chosen foraging routes. Based upon the species studied, commuting birds appeared to be associating with spatially predictable concentrations of prey, whereas the searching strategy was thought to be used when prey were patchily or unpredictably distributed (Weimerskirch 1998b). For example, throughout the breeding season Black-browed albatrosses *Thalassarche melanophris* at Kerguelen Island forage along the eastern edge of the continental shelf, and this coincides with a northeast meandering of the Antarctic Polar Frontal Zone (PFZ, Waugh & Weimerskirch 1998, Weimerskirch et al. 1997c, Weimerskirch 1998b). In contrast, during the incubation period, Wandering albatrosses forage over pelagic waters in long looping courses far from the breeding colonies, using energy gained from prevailing winds to cover vast distances in search of prey (Weimerskirch et al. 1993, 1997b, Weimerskirch 1998b). While these strategies have been shown to vary both within and between species at different stages of the breeding season (Weimerskirch et al. 1993, Weimerskirch 1998b), it is important to remember that foraging is an ultimate trade-off between the distribution of exploitable resources (which are often markedly influenced by the configuration or dynamics of the physical environment) and the constraints imposed at the nest. Multiple solutions to foraging might therefore likely result.

This study details the foraging locations and strategy of breeding Shy albatrosses *Thalassarche cauta* at three locations in Tasmania, Australia, and assesses their likely interactions with longline fisheries. Shy albatrosses form a significant component of the seabird by-catch in both Japanese and Australian domestic longline fisheries targeting Southern Bluefin tuna within the Australian Fishing Zone (AFZ; Brothers 1991, Gales et al. 1998, Brothers and Foster in press). An estimated 5,000 Shy albatrosses (*T. cauta* and *T. steadi*, in unknown proportions) have been killed in the Japanese portion of the fishery alone in the past decade (Gales et al. 1998). Previous work has indicated that adult Shy albatrosses are sedentary and they forage in neritic waters off southeast Australia during their breeding and non-breeding periods (Brothers et al. 1997, 1998, and Chapter 3). While the foraging locations of this species have been previously studied, work was limited to two of the breeding sites and to a single season.

Few studies have reported on the degree of consistency in the foraging zones of albatrosses either between consecutive foraging trips, between breeding stages, or years (but see Hunt et al. 1998). In terms of albatross conservation, however, these assessments seem critical, as the data gathered in satellite tracking studies are used both by conservation and fisheries management agencies to evaluate the potential risk fishing imposes on different populations. As such, this study reports results from a multi-year that was designed primarily to address these issues. Earlier work (Brothers et al. 1998, and Chapter 3) indicated that the populations breeding north (Albatross Island) and south (Pedra Branca) of Tasmania likely had separate foraging zones throughout the year. Separation of the foraging zones, coupled with spatial variation in seabird mortality rates (Gales et al. 1998), caused speculation that longline fisheries were more seriously impacting the albatrosses breeding south of Tasmania (at Pedra Branca and Mewstone). Detailed analyses of foraging zone use for the Albatross Island and Pedra Branca populations are provided, along with the first reports on the distribution of breeding birds from Mewstone. For each population, the extent of overlap with both the Japanese and Australian domestic longline fisheries is detailed.

8.2 METHODS AND MATERIALS

8.2.1 *Species and study sites*

Revisions to albatross taxonomy have elevated the Shy albatrosses breeding in Australia to full species status (Nunn et al. 1996, Robertson & Nunn 1998). The albatrosses breed at three localities; Albatross Island (40.375° S, 144.656° E) in western Bass Strait, which has 5,000 breeding pairs per year, and Pedra Branca (43.867°S, 146.967°E) and Mewstone (43.742°S, 146.375°E) off Tasmania's south coast, where 250 and 7,000 pairs, respectively, breed each year. Breeding is annual, beginning when birds are 5 years of age (N. Brothers, unpubl. data). Egg-laying commences in September, and following a 70 day incubation period, the single chick hatches in December. During incubation and the 3-4 week brooding periods, parents alternate shifts on the nest with foraging trips to sea. The post-brood period of parental care continues for a further 14-16 weeks, and fledging typically occurs in April (N. Brothers, unpubl. data). After departing the colonies, young birds spend at least the next two years at sea.

8.2.2 *Field protocol*

The distribution of the birds at sea was determined using the ARGOS system (Toulouse, France). Birds at Albatross Island were studied during incubation and chick-brooding in

1995/96 and 1996/97, and during post-brood chick-rearing in 1996/97. Birds from the southern colonies were studied in 1997/98; during the incubation period at Pedra Branca, and spanning chick-brood to fledging at Mewstone. Satellite packs were attached to the birds only at nest changeovers, and the individual about to commence a foraging trip was always chosen. The sex of the birds was determined by measuring the width of the head and the upper bill depth (Hedd et al. 1998 and Chapter 2). Birds were banded with a stainless steel band on their left leg, a darvic colour band on their right leg (at Albatross Island), and they were colour-marked with an individually identifiable pattern on the breast (using Dulux hi-gloss enamel spray paint). Satellite transmitters were attached directly to feathers in the centre of the birds back using TESA® tape. Telonics ST10 (85g; 9.0 cm long x 4.2 cm wide x 1.7 cm high, representing 1.9-2.4% of adult body mass) and Toyocom 2038C Platform Terminal Transmitters (PTTs, 120 g; 13.0 cm long x 3.5 cm wide x 1.8 cm high; 2.6-3.4% adult body mass) were used at Albatross Island, while just Telonics transmitters were used at Pedra Branca. The PTTs ran continuously, at either 60 or 90 second repetition rates for between 25 and 30 days. Microwave Telemetry Pico PTTs (38g; 6.8 cm long x 3.5 cm wide x 1.5 cm high, 0.8-1.1% adult body mass), duty-cycled at 10 h on/22 h off were used at Mewstone. For these transmitters, signals were transmitted every 60 s when on, and the devices ran for approximately five months. Details of the numbers of transmitters used and their deployment schedules are listed in Table 8.1.

Table 8.1: Deployment schedules of satellite transmitters on Shy albatrosses from three breeding sites in Tasmania, 1995/96 to 1997/98.

Site	Year	Months	Stage	No. txs[1]	No. birds (pairs)	No. foraging trips per bird	Total foraging trips
Albatross Island	1995/96	September-October	Early incubation	3	4	2 - 5	15
		December	Chick-brooding	4	6 (1)	4 - 13	44
		January	Early chick-rearing	1	1	3	3
	1996/97	October	Early incubation	3	3	3	9
		December	Chick-brooding	6	10	2 - 8	46
		January	Early chick-rearing	4	4	1 - 15	26
Pedra Branca	1997/98	November-December	Early incubation	4	4 (1)	2 - 6	16
Mewstone[2]	1997/98	December	Chick-brooding	2[2]	2[2]	-	-
		January	Early chick-rearing	2	2	-	-
		February-April	Late chick-rearing	2	2	-	-

[1]txs=transmitters; [2]there were two total transmitters at Mewstone, the same two individuals being studied from chick-brood through to fledging.

At Albatross Island, the foraging trip durations of birds carrying satellite packs were calculated partially using satellite locations, but primarily from visual colony attendance checks made every 2-3 hours during daylight. Foraging trip durations were calculated from the first time birds were observed absent from the colony (or when a consistent

satellite location was obtained away from the Island) until they were subsequently observed at the nest site. Inaccuracies using such calculations could be substantial (as much as 9-10 hours), but as the biases were equally likely to be shorter or longer than actual trip durations, the errors would have likely equaled out over time.

All previous attempts to satellite track Shy albatrosses during late chick-rearing have resulted in nest desertions (Brothers et al. 1998 and Chapter 3). In an effort to both minimize disturbance and maximize the chances of successfully recovering satellite packs, in January 1997 two transmitters were deployed within days of the end of chick-brooding, and just hours prior to our leaving the Island. Foraging trip durations for these birds and for the birds studied at Pedra Branca were calculated from the midpoint of locations when birds were heading towards and then away from the Islands. Birds spend little time in the colony after the brooding period has ended, returning ashore only to feed chicks (Chapter 5), and it was therefore rare to obtain satellite locations when the birds were actually on land. Inaccuracies in trip durations calculated in this manner were dependent on the time between successive locations. As this was generally short (with an average of 8 locations a day), biases were likely to have been minimal. Again, though, as the biases were equally likely in both directions, they should have equaled out over time. As the satellite packs deployed at Mewstone were duty-cycled the data could not be partitioned into discrete foraging trips, and were used instead to identify areas of the ocean used during different times of the year.

8.2.3 *Management of the satellite tracking data*

ARGOS diagnostic and dispose files were run through Wildlife Computers SATPAK30 software (version 3.0, Redmond, Washington, USA), which consolidates and validates the files into a single record. Foraging trips with 15 or more locations at sea (76% of the trips) were filtered using an adapted version of the velocity averaging filter of McConnell et al. (1992). The maximum expected rate of travel (27.8 km/h) was estimated using ARGOS positions of known accuracy (location classes 1-3, Brothers et al. 1998, and Chapter 3). Locations resulting in mean travelling speeds greater than 30 km/h were therefore rejected. As the filtering algorithm required a minimum of five locations to filter a single location, 15 locations was arbitrarily chosen as the minimum sample size for application of the filter. Remaining locations (24% of the trips) were iteratively filtered, and locations between which traveling speeds exceeded 30 km/h were again rejected.

Characteristics of the foraging trips were described in two ways: 1) according to their

maximum foraging range, which refers to the distance from the breeding colony to the location obtained furthest afield, and 2) according to the total distance covered per trip, which is simple sum of the distances moved between all locations. To overcome problems of statistical independence, mean values were used for individuals (when information was available for more than one foraging trip) to compare foraging trip characteristics between breeding sites, stages and years. To estimate the 'directness' of travel, the maximum foraging range was also calculated as a percentage of the total distance covered on each foraging trip. This estimate was compared across stages of the breeding season using a nested ANOVA (birds nested within breeding stage).

8.2.4 *Travelling behaviour, foraging effort and patterns of activity at sea*

Rates of travel between successive (filtered) locations were calculated and used to compare traveling speeds across stages of the breeding season and between night and day using nested ANOVAs (birds nested within breeding stage or time of day, as appropriate). As rates of travel between successive locations were not normally distributed, data were log-transformed prior to analysis.

At Albatross Island and at Pedra Branca where satellite transmitters ran continually, the distances the birds traveled during the day and at night were also calculated for each day spent at sea. As the spatial resolution of the satellite locations did not allow calculation of movements during the relatively brief twilight periods, each day was divided into just day and night. Daytime commenced with nautical twilight in the morning (defined as the instant when the sun is at a depression angle of 12° below the horizon) and ended with nautical twilight in the evening. Nighttime was the intervening period. As the day-length varied during and between study periods, and as the timing of locations was not constant between days, distances were corrected for the period of time they covered, resulting in average rates of travel per hour (total distance covered during the daytime or nighttime periods divided by time). This analysis provided a measure of foraging "effort" that was compared across time of day (using a Wilcoxon matched pairs test), years, breeding stages and sites (using nested ANOVAs).

Using this measure of foraging effort, average rates of travel at night were also examined relative to moon phase. The lunar cycle was divided into three phases; 1) full moon, including three days either side of the full moon, 2) new moon, including three days either side of the new moon, and 3) the remaining two weeks when the moon was in quarter or three-quarter phase. Data were examined using nested ANOVA.

Tubular shaped wet/dry activity recorders (4.4 cm long x 1.7 cm diameter, Francis Scientific Instruments, Cambridge, UK) were also used to provide fine scale temporal information regarding how the albatrosses allocated their time at sea. The loggers provided a record of the birds activity (0=flying, 1=sitting on the water) once every 16 s during their foraging trips. Recorders were sewn into padded Velcro bands (final weight 16 g , 0.4-0.5% body mass) and attached to the birds right leg. They were deployed from Albatross Island during incubation and chick-brooding in 1996/97, and results were obtained for between one and six successive trips for each bird.

The following behavioural information was obtained from the activity records:

1) the proportion of time spent flying and sitting on the water during the day and night (as defined above);

2) the number of landings on the water per hour. Landings were identified when the state changed from 0 to 1. Note that landings lasting less than 16 seconds could have been missed using the chosen sampling protocol;

3) the duration of each wet and dry bout. An activity "bout" (either wet or dry) commenced each time a change of state was recorded (from wet to dry, or vice versa).

Differences during the day and night in the proportion of time spent on the water was assessed using repeated measures ANOVA (separately for each stage), and differences between the breeding stages were assessed using nested ANOVAs (birds nested within breeding stage).

The degree of nocturnal activity (the proportion of the night spent flying and the average number of landings per hour) was also analysed relative to 1) moon phase, using one-way ANOVA and 2) wind strength using Spearman rank regression analyses (with analyses run separately during the day and night). Information on wind strength was available once every three hours, and activity data were summarized using the reading as the midpoint. For example, activity data collected between 10 am and 12 pm were summarized to correspond with the 11 am wind reading. Relationships were assessed separately for each breeding stage and according to the time of day (day or night). Information on wind strength was available from a series of automatic weather stations positioned around the coastline of Tasmania, and obtained from the Bureau of Meteorology, Hobart. Wind data from the station closest to the centre of the birds foraging activity at sea were used; during incubation data were used from the weather

station at the King Island airport, and during chick brood from the station at Cape Grim on Tasmania's northwest coast.

The distribution of the duration of wet and dry bouts was compared between breeding stages and time of day using the Chi-square test statistic.

8.2.5 *Characterization of the foraging zones and time allocation along foraging trips*

A suite of analysis programs (developed by C. Sidot, and V. & J. Klinger, CNRS, France), were used to identify areas along the foraging routes where birds spent the majority of their time. The birds position at-sea was estimated every 10 minutes assuming that traveling speed was constant and linear between each satellite-derived location (Weavers 1992). Each foraging trip was, in turn, entered into a second program where a user defined grid matrix was imposed over the locations and the proportion of time the birds spent in each grid square was calculated. To separate areas used for foraging from those used for travelling, the median amount of time birds spent per grid square (on each foraging trip) was calculated and used as a threshold value. Areas for which values lay beyond the threshold were considered to lie within the foraging zone. In the absence of validation with albatrosses, this interpretation was based upon Bost et al.'s (1997) study of King penguins *Aptenodytes patagonicus*. Using stomach temperature sensors and satellite transmitters in tandem, they established a strong association between areas where penguins spent most of their time and areas where most of their food was ingested.

Analysis of time spent per grid square was used to examine:

1) concentrated areas of activity which may have represented the foraging zones;

2) the size of these foraging zones during different stages of the breeding season;

3) the degree of foraging zone overlap at the following temporal scales;

    a) between the successive foraging trips of an individual bird,

    b) between the different individuals studied contemporaneously,

    c) between the different stages or years in which an individual was repeatedly studied, and

    d) at the "population" level, with data for contemporaneously studied individuals pooled to represent the foraging zone of the population as a whole. Population

level data were used to assess the degree of consistency in foraging zone use between different breeding stages and years. Satellite tracking data collected during 1993/94 at Albatross Island and during 1994/95 at Pedra Branca (Brothers et al. 1998, and Chapter 3) were reassessed here to allow for more extensive inter-annual comparisons.

Because a great degree of interpolation was required to conduct the analyses described above, trips were analysed in this manner only when a minimum of five locations was received at sea. Overlap analyses were conducted only within the identified foraging zones, and figures are presented as means. For example, overlap between foraging trips "A" and "B" was calculated as the mean overlap of trip "A" on "B" and trip "B" on "A". Overlap analyses were conducted at two spatial scales; 1) a fine scale, with grid squares 0.05° x 0.05° (approximately 5 km x 5 km); this level approached the accuracy of the satellite locations themselves (Brothers et al. 1998, and Chapter 3), and 2) at a broad scale, with grids 0.25° x 0.25° (approximately 25 km x 25 km). The fine scale assessed whether birds returned to the same physical location to feed from one trip to the next, as might be expected if they were cueing on topographical features such as sea mounts or shelf breaks which tend to reliably concentrate prey. The broad scale assessed whether foraging was random (ie, in direction from the colony), and whether the birds foraged in the same general (but not necessarily specific), areas from one trip to the next. Consistency in broad foraging areas might be expected if prey were mobile (through either self propulsion or planktonic dispersal) and were likely to move substantially between foraging trips. The spatial resolution of the large scale was ultimately limited by the size at which meaningful inter-trip comparisons could be made during chick-brood, when the birds feed within 100 km of the colonies (Brothers et al. 1998 and Chapter 3).

8.2.6 *Oceanographic features of the foraging zones*

Contemporaneous satellite-derived estimates of sea-surface temperature (SST) were obtained for the southeast Australian region approximately once every 10 days during the tracking sessions. Data were weekly compilations of daily or twice daily passes, which were overlaid and median filtered by the CSIRO's Division of Remote Sensing in Hobart. Estimates of SST were obtained at a spatial resolution of 3.3 km x 3.3 km.

8.2.7 *Interactions with and the influence of fisheries*

The at-sea distribution of the birds was analyzed for potential interactions with both the Japanese and Australian domestic longline fisheries for Southern Bluefin Tuna in the

AFZ. As in Brothers et al. (1998) fishing effort was defined as the number of hooks set in each 1° x 1° grid square. Data on fishing effort was provided by the Australian Fisheries Management Authority.

Longline fisheries have the most serious impact on albatross populations, but at-sea distributions of birds are also known to be influenced by other fishing practices where baits and offal are available for scavenging (Ryan & Moloney 1988). The influence of such processes was explored by examining correspondence between albatross foraging zones and the distribution of effort in relevant fisheries around Tasmania. Those of greatest potential influence include the South-east Trawl, the Southern Rock Lobster *Jasus edwardsii*, and the various Finfish fisheries. For the trawl fishery, effort was provided either as the number of boats operating or the total hours spent trawling in each 1° x 1° grid square per month. For reasons of confidentiality the latter measure of effort could be provided only where five or more boats had operated. In both the Rock Lobster and the Finfish fisheries effort was provided as the total number of vessel days fished in each grid square per month. Rock lobster effort data was available from 1993, however, accurate records were available for the Finfish fisheries only from March of 1995. Data were obtained from the Australian Fisheries Management Authority (South east trawl fishery) and the Tasmanian Department of Primary Industry and Fisheries (other fisheries).

8.3 RESULTS

8.3.1 *General description of the data*

A total of 2,110, 607 and 479 locations were received while birds from Albatross Island, Pedra Branca and Mewstone, respectively, were foraging at sea. After filtering, 1,930 (91.5%), 551 (90.8%) and 397 (82.7%) locations remained at each site. For transmitters that ran continuously, 8 ± 2.2 locations were received per day (n=396 tracking days), but with the duty-cycling at Mewstone, just 2 ± 1.5 locations were received per day (n=243 tracking days). Locations were also not equally probable during the day, coincident with satellite coverage at 40° south, with relatively few locations available between 09:00 and 13:00 h local time (Figure 8.1). The time between successive locations influenced estimated rates of travel, with increasing underestimates of traveling speed resulting from locations that were further apart ($F_{3,2909}$=66.4, $p < 0.001$, also Brothers et al. 1998 and Chapter 3). Specifically, estimates of traveling speed from locations less than two hours

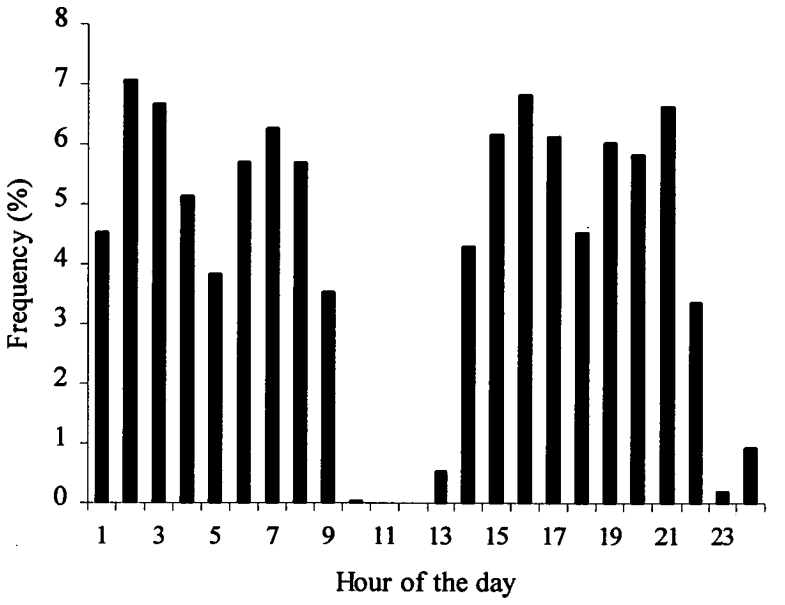


Figure 8.1. Histogram of the local time of satellite locations received for Shy albatrosses from Albatross Island, Pedra Branca and Mewstone between 1995 and 1998.

apart (13.4 ± 0.30 km/h) were significantly greater than locations at all other temporal resolutions (2-4h, 9.6 ± 0.48 km/h, 4-6h, 6.2 ± 1.12 km/h, and 6 + h, 4.1 ± 0.67 km/h; Tukey's HSD $p < 0.05$). Because of this, comparison of rates of travel were explored using locations spaced by less than two hours (n=1,204 at Albatross Island, n=201 at Pedra Branca, and n=152 at Mewstone), or by using all locations to construct mean hourly rates of travel, assuming that variation caused by locations at different temporal resolutions averaged out over time.

8.3.2 *Effect of carrying satellite packs*

At Albatross Island, all birds fitted with satellite transmitters during incubation and chick-brooding continued breeding, and returned to the colony at regular intervals to change shifts at the nest. Attempts to study the birds after the brooding period had ended, however, were not as successful. While the two birds studied in 1996/97 initially fed their chicks, they subsequently abandoned the breeding attempt after carrying the packs for 21 and 28 days. The partners of these two birds continued feeding the chicks, however, and both chicks were healthy at banding some eight weeks later. Both adults were sighted in the colony the following winter, but the satellite packs had already been lost.

As deployments at Pedra Branca and Mewstone were made during brief visits to the Islands in 1997/98, less was known of the effects of the deployments on breeding outcomes. However, three of the four study nests at Pedra Branca failed within three weeks, and just one of the birds continued breeding during the month-long deployment. At Mewstone, where the packs were smaller, and deployed earlier in the season, both birds appeared to continue breeding. Adults remained within the vicinity of the colony over the next 3-4 months, and regularly returned there until fledging in March/April. A portion of the post-breeding movements of one of these birds was also obtained. While this pack remained attached for 137 days, the other apparently detached mid-March, three weeks before to the end of the breeding season (after 105 days). Battery voltage was constant for both transmitters when signals ceased, indicating that it was likely the attachment (and not the transmitters) that had failed.

The foraging trip durations of birds carrying satellite packs were significantly longer than birds that carried leg-mounted VHF transmitters (20 g, 0.4-0.6% body mass) in each tracking session from Albatross Island with the exception of incubation in 1995/96 (Table 8.2). While at Pedra Branca the foraging trip durations of birds carrying the different

types of transmitters were similar (Table 8.2), the small sample sizes (5 vs. 4) provided limited power to detect potential differences.

Table 8.2: Comparison of the foraging trip durations of Shy albatrosses which were carrying satellite packs or leg-mounted VHF transmitters.

Site	Stage	Year	Satellite packs (n)	VHF transmitters (n)	T test
Albatross Island	Incubation	95/96	2.4 ± 0.73 (4)	1.7 ± 0.82 (10)	t=-1.48, p=0.166
		96/97	3.5 ± 0.31 (3)	2.3 ± 0.73 (20)	t=-2.65, p=0.015
	Chick-brooding	95/96	1.2 ± 0.28 (6)	0.9 ± 0.21 (16)	t=-2.25, p=0.036
		96/97	1.1 ± 0.20 (10)	0.9 ± 0.12 (20)	t=-4.58, p=0.000
	Early chick-rearing	96/97	2.3 ± 0.57 (2)	1.0 ± 0.28 (20)	t=-5.90, p=0.000
Pedra Branca	Incubation	97/98	2.0 ± 0.85 (5)	2.8 ± 0.91 (4)	t=1.42, p=0.197

8.3.3 *Foraging trip characteristics*

8.3.3.1 *Albatross Island*

Descriptive statistics for the distances traveled and the duration of foraging trips for each individual studied at Albatross Island in 1995/96 and 1996/97 are given in Table 8.3. There were no differences between years in the duration, maximum foraging range or the total distances covered on foraging trips during either incubation ($F_{1,5}$=5.2, $p > 0.05$; $F_{1,5}$=0.3, $p > 0.05$; and $F_{1,5}$=0.8, $p > 0.05$, respectively) or chick-brooding ($F_{1,14}$=0.1, $p > 0.05$; $F_{1,14}$=0.6, $p > 0.05$; $F_{1,14}$=0.8, $p > 0.05$, respectively). With the exception of three trips of a single bird in 1995/96, foraging areas past the end of chick brood were studied only in 1996/97.

Given that there were no differences between years in foraging trip characteristics, data from both years were combined to evaluate differences between the breeding stages. The duration of foraging trips, the maximum foraging ranges and the total distances traveled varied across the breeding season (Table 8.3, $F_{2,25}$= 30.9, $p < 0.001$; $F_{2,25}$=20.1, $p < 0.001$, $F_{2,25}$=44.2, $p < 0.001$). During incubation, foraging trips were longer (2.8 ± 0.72 days), birds traveled further from the breeding colony (180 ± 36.9 km) and they covered greater total distances than during any other stage of the breeding season (Tukey's HSD $p < 0.05$, for all). Trips were shortest and birds foraged closest to the islands when they were brooding chicks (Table 8.3). In the month after chicks were left alone at the nest (early chick-rearing), foraging trip characteristics again increased (trips 1.8 ± 0.62 days, foraging range 119 ± 15.5 km, distance traveled 426 ± 155.6 km), but not to the extent

Table 8.3: Details of the individual Shy Albatrosses satellite tracked from Albatross Island, and the characteristics of their foraging trips during the 1995-96 and 1996-97 breeding seasons.

Breeding stage	Year	Individual (Colour band#)	Sex	No. filtered locations at sea	No. foraging trips	Foraging trip duration (d) Mean ± SD (range)	Foraging range (km) Mean ± SD (range)	Distance covered (km) Mean ± SD (range)
Incubation	1995	133*	Male	82	5	2.1 ± 0.92 (0.7 - 3.0)	200 ± 92.7 (59 - 297)	817 ± 432.1 (211 - 1334)
	1995	135*	Male	50	3	1.7 ± 0.21 (1.5 - 1.9)	129 ± 11.1 (119 - 141)	418 ± 34.8 (381 - 450)
	1995	130	Male	65	2	3.4 ± 0.50 (3.0 - 3.7)	227 ± 47.4 (193 - 260)	888 ± 5.7 (884 - 892)
	1995	YYRL	Male	121	5	2.5 ± 0.93 (1.2 - 3.6)	134 ± 42.8 (84 - 196)	689 ± 393.9 (202 - 1265)
	1996	133	Male	100	3	3.4 ± 1.21 (2.1 - 4.5)	206 ± 57.6 (162 - 271)	818 ± 266 (514 - 1006)
	1996	121	Male	106	3	3.8 ± 0.15 (3.7 - 4.0)	171 ± 21.2 (147 - 188)	921 ± 65.2 (847 - 969)
	1996	092	Female	81	3	3.2 ± 1.30 (1.7 - 4.0)	190 ± 93.9 (86 - 269)	730 ± 365.9 (314 - 1002)
Incubation mean						**2.8 ± 0.72**	**180 ± 36.9**	**754 ± 169.1**
Chick-brooding	1995	133	Male	98	13	0.9 ± 0.48 (0.3 - 2.2)	55 ± 31.8 (12 - 103)	148 ± 71.5 (24 - 294)
	1995	135	Male	45	7	0.9 ± 0.30 (0.4 - 1.3)	93 ± 41.2 (30 - 145)	236 ± 120.5 (64 - 424)
	1995	117*	Male	36	4	1.3 ± 0.50 (0.6 - 1.6)	103 ± 51.4 (35 - 157)	253 ± 129.3 (71 - 357)
	1995	129	Female	46	7	1.0 ± 0.18 (0.7 - 1.3)	132 ± 57.0 (49 - 208)	336 ± 122.2 (151 - 516)
	1995	115	Female	116	9	1.3 ± 0.42 (0.6-1.9)	108 ± 39.6 (31 - 163)	330 ± 170.5 (80-690)
	1995	114	Female	52	4	1.6 ± 0.71 (0.8 - 2.5)	82 ± 2.6 (80 - 86)	300 ± 119.2 (215 - 476)
	1996	117	Male	35	5	0.8 ± 0.15 (0.6 - 1.0)	76 ± 46.5 (34 - 156)	211 ± 105.2 (87 - 377)
	1996	129	Female	35	4	1.0 ± 0.17 (0.8 - 1.2)	112 ± 44.8 (53 - 162)	279 ± 124.0 (124 - 422)
	1996	055	Male	51	6	1.1 ± 0.34 (0.7 - 1.6)	85 ± 35.6 (45 - 129)	245 ± 80.6 (91 - 327)
	1996	Red RL	Female	34	4	1.1 ± 0.15 (1.0 - 1.3)	73 ± 27.5 (45 - 107)	220 ± 73.7 (149 - 308)
	1996	054	Male	24	2	1.5 ± 0.10 (1.4 - 1.6)	131 ± 5.7 (127 - 135)	359 ± 29.0 (338 - 379)
	1996	067	Female	39	5	0.9 ± 0.18 (0.6 - 1.1)	85 ± 31.4 (52 - 136)	256 ± 110.7 (163 - 440)
	1996	053	Male	32	4	1.3 ± 0.42 (1.0 - 1.9)	92 ± 18.6 (65 - 108)	294 ± 101.9 (202 - 439)
	1996	052	Male	44	4	1.2 ± 0.25 (1.0 - 1.5)	147 ± 38.1 (114 - 196)	355 ± 69.7 (301 - 457)
	1996	064	Male	55	5	1.2 ± 0.44 (0.5 - 1.7)	87 ± 38.5 (19 - 119)	232 ± 109.6 (48 - 322)
	1996	063	Male	45	7	1.2 ± 0.40 (0.7 - 1.7)	137 ± 63.7 (57 - 230)	313 ± 166.4 (118 - 576)
Chick-brooding mean						**1.1 ± 0.23**	**100 ± 26.0**	**273 ± 58.3**
Early	1995	115	Female	23	2	1.0 ± 0.91(0.3-2.0)	100 ± 90.7 (31 - 203)	297 ± 346.8(65 - 696)
chick-rearing	1996	048	Male	257	15	1.9 ± 1.29 (0.6 - 4.3)	126 ± 47.9 (44 - 230)	449 ± 302.4 (117 - 1011)
	1996	049	Female	230	9	2.7 ± 1.68 (1.1 - 6.6)	122 ± 27.6 (80 - 126)	561 ± 256.9 (212 - 918)
	1996	063	Male	13	1	2.0	140	587
	1996	054	Male	12	1	1.6	109	237
Early chick-rearing mean						**1.8 ± 0.62**	**119 ± 15.5**	**426 ± 155.6**

* indicates that the individual was subsequently re-tracked

exhibited during incubation. No differences in the foraging characteristics of adult males and females were apparent during chick-brood, and this was the only stage where there were sufficient numbers of individuals to make such comparisons.

Foraging trip duration was related to both the total distance traveled (Spearman R=0.88, $p < 0.00001$), and the maximum foraging range (Spearman R=0.77, $p < 0.00001$; Figure 8.2). On foraging trips during chick-brood, the maximum foraging range constituted 37.7 ± 9.0 % (n=95) of the total distance traveled, and this percentage was higher than at any other stage in the breeding season (incubation trips, 25.3 ± 6.9%, n=24; chick-rearing trips, 30.9 ± 11.3%, n=23; $F_{2,19}=14.5$, $p < 0.001$; Tukey's HSD $p< 0.001$). During this stage birds seemed to return to the colony immediately after finding food.

8.3.3.2 *Pedra Branca and Mewstone*

Foraging trip characteristics for the birds studied on Pedra Branca and Mewstone are given in Table 8.4. During incubation Pedra Branca birds spent 2.8 ± 0.91 days at sea, traveled 88 ± 13.8 km from the Island, and covered 517 ± 135.0 km on their foraging trips. Because of transmitter duty-cycling, only maximum foraging ranges were available for Mewstone birds. During brood and early chick-rearing these birds moved 115 ± 36.8 km and 105 ± 10.6 km, respectively from the colony. Foraging ranges were somewhat extended later in the season, with birds ranging up to 176 ± 31.8 km from the colony (Table 8.4).

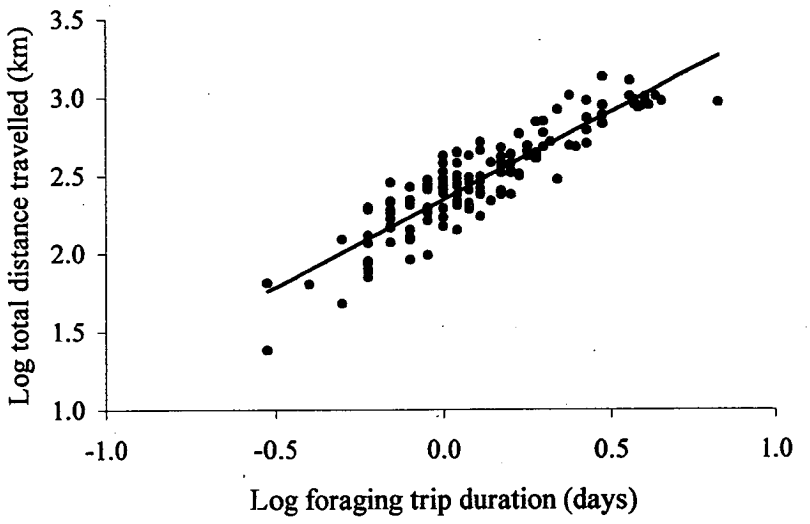
At Pedra Branca, foraging trip durations were related to the total distance traveled (Spearman R=0.89, $p < 0.00001$), but there was no relationship between foraging trip duration and maximum foraging range (Spearman R=0.44, p=0.092).

8.3.3.3 *Comparison between sites*

Foraging trip durations were similar at Albatross Island and Pedra Branca during incubation (t=0.14, df=9, p=0.893), but birds from Albatross Island moved further from the colony and traveled greater total distances in search of food (t=4.67, df=9, p=0.001, and t=2.39, df=9, p=0.040). Similar maximum foraging ranges at Albatross Island and Mewstone indicated that at least when rearing chicks, birds fed at similar distances from their colonies (t=0.75, df=16, p=0.46, and t=0.68, df=5, p=0.526, Tables 8.3 & 8.4).

8.3.4 *Rates of travel and foraging effort*

A.



B.

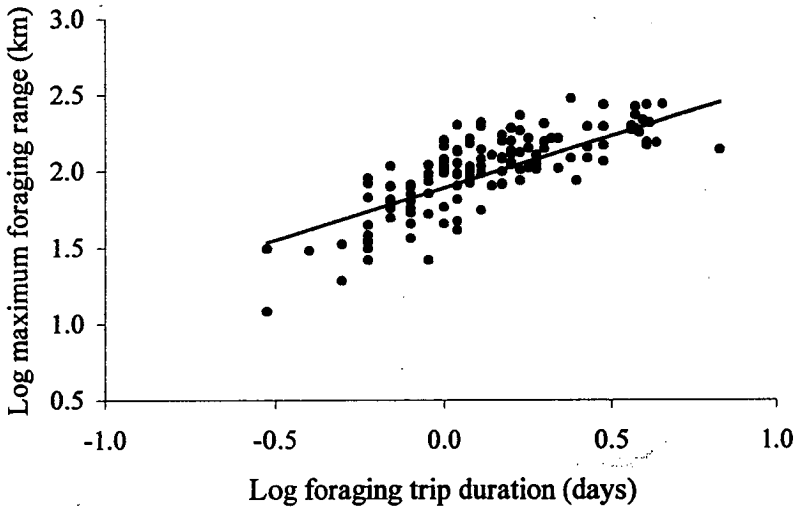


Figure 8.2: Relationship between log of foraging trip duration and (A) log of the total distance traveled and (B) log of the maximum foraging range of Shy albatrosses from Albatross Island 1995/96 and 1996/97.

Table 8.4: Details of the individual Shy albatrosses satellite tracked from Pedra Branca and Mewstone in 1997/98, along with characteristics of their foraging trips during each breeding stage. Because Mewstone satellite transmitters were duty-cycled (10 hr on and 22 hr off), only the maximum foraging ranges are available.

Breeding site	*Stage	Individual	No. filtered locations at sea	No. foraging Trips	Foraging trip duration (d) Mean ± SD (range)	Maximum foraging range km) Mean ± SD (range)	Distance covered (km) Mean ± SD (range)
Pedra Branca	I	1	98	6	2.7 ± 1.19 (1.1 - 4.0)	109 ± 20.6 (95 - 150)	556 ± 262.2 (263 - 917)
Pedra Branca	I	2	140	4	4.1 ± 1.10 (3.0 - 5.5)	82 ± 20.6 (68 - 112)	611 ± 255.8 (331 - 910)
Pedra Branca	I	3	69	4	2.0 ± 1.21 (0.9 - 3.1)	81 ± 43.6 (39 - 130)	317 ± 206.7 (91 - 514)
Pedra Branca	I	4	34	2	2.4 ± 1.63 (1.2 - 3.5)	81 ± 62.2 (37 - 125)	583 ± 653.4 (121 - 1045)
Pedra Branca Incubation mean					**2.8 ± 0.91**	**88 ± 13.8**	**517 ± 135.0**
Pedra Branca	P	1	93	-	18	610	2788
Pedra Branca	P	3	35	5	1.0 ± 0.43 (0.5 - 1.5)	28 ± 6.7 (19 - 36)	106 ± 55.6 (43 - 196)
Pedra Branca	P	4	61	7	1.5 ± 0.52 (1.0 - 2.5)	84 ± 43.6 (20 - 140)	319 ± 242.3 (92 - 688)
Mewstone	B	1203	36	-	-	89	-
Mewstone	B	1204	47	-	-	141	-
Mewstone Chick-brooding mean			-	-	-	**115 ± 36.8**	-
Mewstone	ECR	1203	53	-	-	112	-
Mewstone	ECR	1204	49	-	-	97	-
Mewstone Early chick-rearing mean				-	-	**105 ± 10.6**	-
Mewstone	LCR	1203	135	-	-	198	-
Mewstone	LCR	1204	61	-	-	153	-
Mewstone Late chick-rearing mean				-	-	**176 ± 31.8**	-
Mewstone	P	1203	13	-	-	358	-

* I = Incubating, P= Post-breeding, B = Chick-brooding, ECR = Early chick-rearing, LCR = Late chick-rearing

8.3.4.1 *Albatross Island*

Using only locations spaced by less than two hours, rates of travel were similar across stages of the breeding season (incubation, 17 ± 19.8 km/h, n=365; chick-brood, 15 ± 11.7 km/h, n=515; chick-rearing 14 ± 10.3 km/h, n=324; $F_{2,23}$=0.1, $p > 0.05$), but differed according to time of day, with birds traveling faster during the day (16 ± 15.7 km/h, n=883) than at night (12 ± 9.7 km/h, n=319; $F_{1,39}$=6.9, $p < 0.05$).

Expressing foraging effort as the average distance moved per hour, there were no differences in foraging effort between years, or between stages of the breeding season during either the day (years: 1995/96, 12 ± 5.1 km/h, n=49 days; 1996/97, 11 ± 3.8 km/h, n=107 days; $F_{1,21}$=0.002, $p > 0.05$; stages: incubation 12 ± 5.1 km/h, n=46; chick-brood, 11 ± 3.8 km/h, n=61; chick-rearing 10 ± 3.9 km/h, n=49; $F_{2,153}$=1.08, $p > 0.05$) or the night (years: 1995/96, 9 ± 7.1 km/h, n=49 days; 1996/97, 8 ± 5.6 km/h, n=107 days; $F_{1,21}$=0.018, $p > 0.05$; stages: incubation 9 ± 6.2 km/h, n=46; chick-brood, 8 ± 6.6 km/h, n=61; chick-rearing 7 ± 5.8 km/h, n=49; $F_{2,153}$=0.71, $p > 0.05$). Average rates of travel per hour, however, did differ according to the time of day, and were greater during the day than at night (11 ± 4.2 km/h vs. 8 ± 6.2 km/h, respectively, Wilcoxon matched pairs test, Z=-5.28, $p < 0.001$).

The proportion of travel undertaken during the daylight hours was also calculated and compared across stages of the breeding season. Just a portion of the above data set could be used for this analysis, as days were included only where at least 80% of a 24 hour period was accounted for by summing data during the day and night. During incubation 74 ± 12.9% (n=24 days) of the distance traveled each day was undertaken during daylight, and this proportion increased to 82 ± 10.5% (n=22 days) and 82 ± 14.9% (n=29 days), during chick-brood and early chick-rearing, respectively (nested ANOVA, $F_{2,16}$=3.63, p=0.050). The proportion of travel occurring during daylight increased from spring through summer (incubation to early chick-rearing) as the number of daylight hours per day increased (Spearman rank regression, R=+0.256, p=0.026, n=75).

8.3.4.2 *Pedra Branca and Mewstone*

Using locations spaced by less than two hours, birds at both Pedra Branca and Mewstone traveled at similar speeds during the day and night (Pedra Branca $F_{1,6}$=0.59, p=0.472, 15 ± 23.5 and 11 ± 7.8 km/h; Mewstone $F_{1,2}$=8.1, p=0.105, 16 ± 11.9 and 12 ± 11.7 km/h). At Mewstone, the rates of travel differed across the breeding season ($F_{2,3}$=9.2, p=0.052)

with birds traveling faster in late than early chick-rearing (chick-brood, 15 ± 13.7 km/h, n=34; early chick-rearing 11 ± 9.0 km/h, n=40; late chick-rearing 17 ± 12.1 km/h, n=73; Tukey's HSD, p=0.050).

8.3.4.3 *Comparison between sites*

Using speeds between locations spaced by less than two hours, and also the average rates of travel per hour across the day and night, birds from all sites traveled at similar speeds during all stages of the breeding season (nested ANOVAs, $p > 0.05$ for all comparisons).

8.3.4.4 *Effect of moon phase on rate of travel at night*

Pooling across sites, the average rate of travel per hour during the night differed according to moon phase ($F_{2,49}=3.71$, $p < 0.05$), with birds traveling faster during the full moon (full moon 10 ± 6.2 km/h, n=49; quarter and three-quarter moon 8 ± 6.4 km/h, n=90; new moon 7 ± 5.3 km/h, n=37, Tukey's HSD $p < 0.05$ for all).

8.3.5 *Pattern of activity at sea*

8.3.5.1 *Proportion of time wet and dry*

On foraging trips during the incubation period birds from Albatross Island spent an average of 31% (range 10-47%) of the day sitting on the water, and 69% of the day flying (range 53-90%, Table 8.5), while at night, 80% (range 67-99%) of the time was spent sitting on the sea, and just 20% flying. During this stage, significantly more of the night than the day was spent sitting on the sea (repeated measures ANOVA, $F_{1,8}=74.2$, $p < 0.001$). Across the whole foraging trip, time was equally allocated between flying and sitting on the water, with values averaging 50% for both. There was, however, substantial day to day, as well as trip to trip variation in the proportion of time spent sitting on the sea, with wet times ranging from 36% to 61% of the total foraging trip duration.

During chick-brood, birds spent 27% (range 4-62%) of the day sitting on the water, and 73% of the day flying (range 38-96%). The proportion of the day spent flying was similar during chick-brood and incubation (nested ANOVA, $F_{1,7}=0.15$, $p > 0.05$). During the night, while brooding, however, birds spent 46% (5-93%) of their time on the water, and 54% flying. Equal proportions of the day and night were spent flying during this stage (73 vs 54%, repeated measures ANOVA, $F_{1,10}=4.21$, $p=0.067$). When brooding chicks, birds also spent more of the night (nested ANOVA, $F_{1,7}=10.54$, $p < 0.05$), and

Table 8.5: Activity patterns of Shy albatrosses from Albatross Island relative to stage of the breeding season and time of day

Bird	Sex	Trip no.	Breeding stage*	Start date	Trip duration (hours)	Daylight		Night time		% of total time at sea sitting on the water
						% of deployment time	% of daylight sitting on water	% of deployment time	% of darkness spent on water	
1	M	1	I	03/10	70.8	60.4	47.1	39.6	68.3	55.5
		2	I	09/10	68.9	60.3	40.2	39.7	67.0	50.7
		3	I	14/10	48.2	63.2	31.9	36.8	73.5	47.3
2	M	1	I	03/10	43.7	57.3	10.1	42.7	69.9	35.6
		2	I	08/10	30.5	66.6	28.8	33.4	99.3	49.1
		3	I	10/10	27.0	66.4	30.5	33.5	72.6	44.6
3	M	1	I	04/10	127.4	63.7	40.1	36.2	97.5	60.8
		2	I	14/10	99.6	64.5	21.4	35.5	77.7	41.3
4**	F	1	I	04/10	32.4	48.3	27.0	51.7	92.0	60.7
Incubation mean							**30.8 ± 11.05**		**79.8 ± 12.17**	**49.5 ± 8.51**
3	M	1	B	16/12	16.0	59.7	3.6	40.3	85.4	36.3
		2	B	17/12	21.5	69.9	9.7	30.1	59.7	24.5
		3	B	19/12	14.8	100	13.1	-	-	13.1
5	F	1	B	20/12	26.8	72.4	13.8	23.7	92.7	32.0
		2	B	23/12	17.5	100	61.8	-	-	61.8
		3	B	25/12	17.7	100	44.4	-	-	44.4
		4	B	26/12	17.8	100	29.6	-	-	29.6
		5	B	27/12	26.5	76.4	35.5	23.6	27.3	33.5
		6	B	29/12	29.8	78.8	9.8	21.2	33.3	14.7
6	F	1	B	17/12	20.2	66.4	28.4	33.6	72.9	42.2
		2	B	19/12	10.3	100	34.4	-	-	34.4
		3	B	20/12	28.3	77.4	11.5	22.6	27.1	15.0
7	F	1	B	22/12	21.1	69.8	13.3	30.2	56.4	26.2
		2	B	23/12	20.8	69.4	35.3	30.6	4.7	25.9
		3	B	24/12	18.4	65.8	41.8	34.2	44.8	42.8
8	M	1	B	27/12	36.9	83.1	40.1	16.9	5.3	34.2
Chick-brooding mean							**26.6 ± 16.41**		**46.3 ± 29.97**	**31.9 ± 12.18**

* I = incubating; B = chick-brooding: ** incomplete trip - recordings ceased part way through first trip

more of the total at-sea time in flight (average 68%; nested ANOVA, $F_{1,7}$=23.95, $p < 0.01$).

However, there was a relationship between the proportion of the night spent flying and the phase of the moon (one-way ANOVA, $F_{2,31}$=3.89, $p < 0.05$), with birds spending significantly more of the night flying when the moon was full (full moon, 62 ± 33.9%, n=6 days, quarter and three-quarter moon, 26 ± 29.5%, n=21, new moon, 23 ± 21.9%, Tukey's HSD $p < 0.05$). While there appeared to be a difference between the incubation and brooding periods in the proportion of the night birds spent in flight, this was actually an artifact of the relationship with moon phase. When data collected during the full moon were excluded (there was a full moon only during the brooding period), there was no difference between the stages in the proportion of the night spent flying (nested ANOVA, $F_{1,4}$=2.43, $p > 0.05$; incubation 21 ± 26.7%, n=23, chick-brooding 44 ± 25.0%, n=5).

During incubation, there was no relationship between wind speed and the proportion of time birds spent flying during the day or the night (Spearman rank correlations; daytime, R=0.182, $p > 0.05$, n=67, nighttime R=0.184, $p > 0.05$, n=38). Also, during brood wind speed had no effect on the proportion of time spent flying during the day (Spearman rank correlations; daytime, R=0.190, $p > 0.05$, n=56), but wind speed was negatively related to the proportion of time spent flying at night (Spearman rank correlations; R=-0.698, $p < 0.05$, n=9). The latter relationship again seems to be an artifact of the relationship with moon phase. That is, birds tended to fly at night during the full moon irrespective of wind speed, but they did not fly at night during other phases, even when the winds were strong. The negative relationship was driven by the fact that winds were weaker at night when the moon was full than when it was in quarter or three-quarter phase (full 6.1 ± 4.6 m/s, vs quarter and three-quarter 9.9 ± 4.3 m/s). Unfortunately there was insufficient data to run a two-way ANOVA.

8.3.5.2 *Water landings*

The number of landings per hour ranged from 0 to 24, with mean hourly rates ranging from 1.0 to 5.5 (Figure 8.3). At no time of the day were the birds inactive, but the relative degree of activity was not constant across the 24-hour period during either incubation or brood (χ^2_{23}= 186.1, $p < 0.01$; χ^2_{23}= 282.2, $p < 0.01$). Birds landed on the water most often during the morning and again in the evening before dark, although the diurnal pattern was more pronounced during chick-brood than during incubation (Figure 8.3). During the brooding period, few landings were made on the water between 02:00h and 04:00h or between 18:00h and 20:00h.

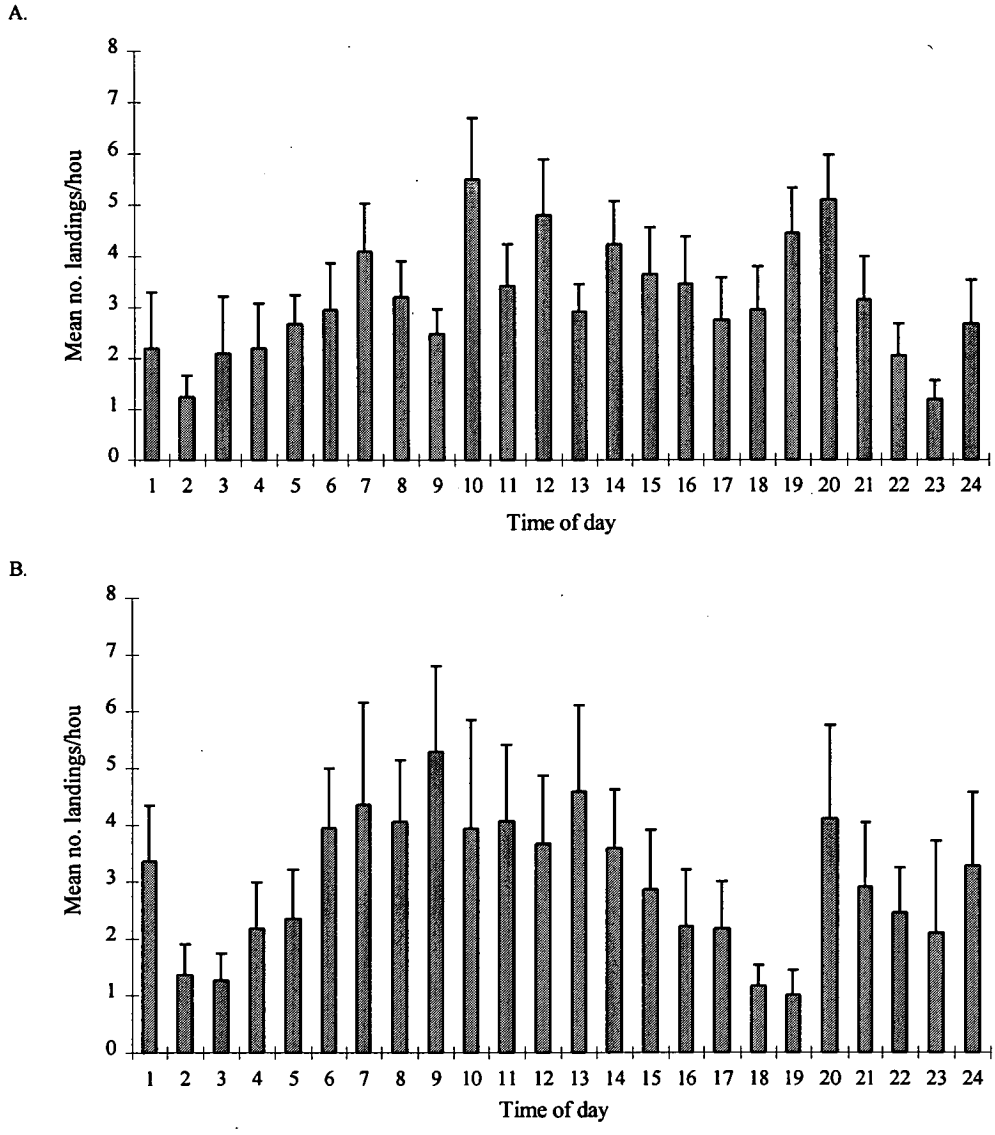


Figure 8.3. Mean number of landings on the water during each hour of the day during the (A) incubation and (B) chick-brooding periods, 1996/97.

At night, there was no relationship between the mean number of landings on the water per hour and moon phase (one-way ANOVA, $F_{2,30}=2.51$, $p > 0.05$). Birds landed equally as often per hour during the night in all phases of the lunar cycle (full moon, 1.1 ± 1.11; quarter and three-quarter phases, 0.7 ± 0.61; new moon, 1.5 ± 1.11).

During incubation there was a negative relationship between the frequency of landings on the water and wind speed during the day (Spearman rank correlation; $R=-0.254$, $p < 0.05$, $n=67$), with birds landing more often when wind speeds were low. However, during chick brood this relationship was positive (Spearman rank correlation; $R=0.282$, $p < 0.05$, $n=56$), with birds landing more often when the wind speed was high. During both stages, however, the relationship was weak and wind speed accounted for less than 6% of the variation in landing frequency. There was no relationship between wind speed and the frequency of landings on the water at night during either stage (Spearman rank correlations; $R=-0.107$, $p > 0.05$, $n=38$, $R=0.204$, $p > 0.05$, $n=9$, for incubation and brooding, respectively).

8.3.5.3 *Distribution of wet/dry bout durations*

The durations of all wet and dry bouts were calculated, and the distribution of these durations compared during the day and night and across stages of the breeding season (Figure 8.4). The distribution of bouts during all periods was dominated by intervals lasting five minutes or less, but these distributions differed with respect to time of day and breeding stage. During incubation the distribution of in-flight bouts differed during the day and night, with longer in-flight bouts predominating during the day ($\chi_7=56.7$, $p < 0.001$; Figure 8.4a). The opposite was obvious for the distribution of wet bouts, with longer wet periods predominating at night ($\chi_7=56.9$, $p < 0.001$; Figure 8.4b). During chick-brooding, the distribution of in-flight bout durations was similar during the day and night ($\chi_7=8.5$, $p > 0.05$; Figure 8.4c), but longer wet periods predominated at night ($\chi_7=24.9$, $p < 0.01$; Figure 8.4d). There were also differences between the breeding stages, with brooding birds spending longer periods flying than incubating birds both during the day and at night ($\chi_7=31.7$, $p < 0.001$; $\chi_7=34.9$, $p < 0.001$). Incubating birds also spent longer periods sitting on the sea during the day ($\chi_7=46.7$, $p < 0.001$), whereas there were no stage differences in the distribution of wet bout durations at night ($\chi_7=11.8$, $p > 0.05$).

8.3.6 *Characteristics of the foraging zones*

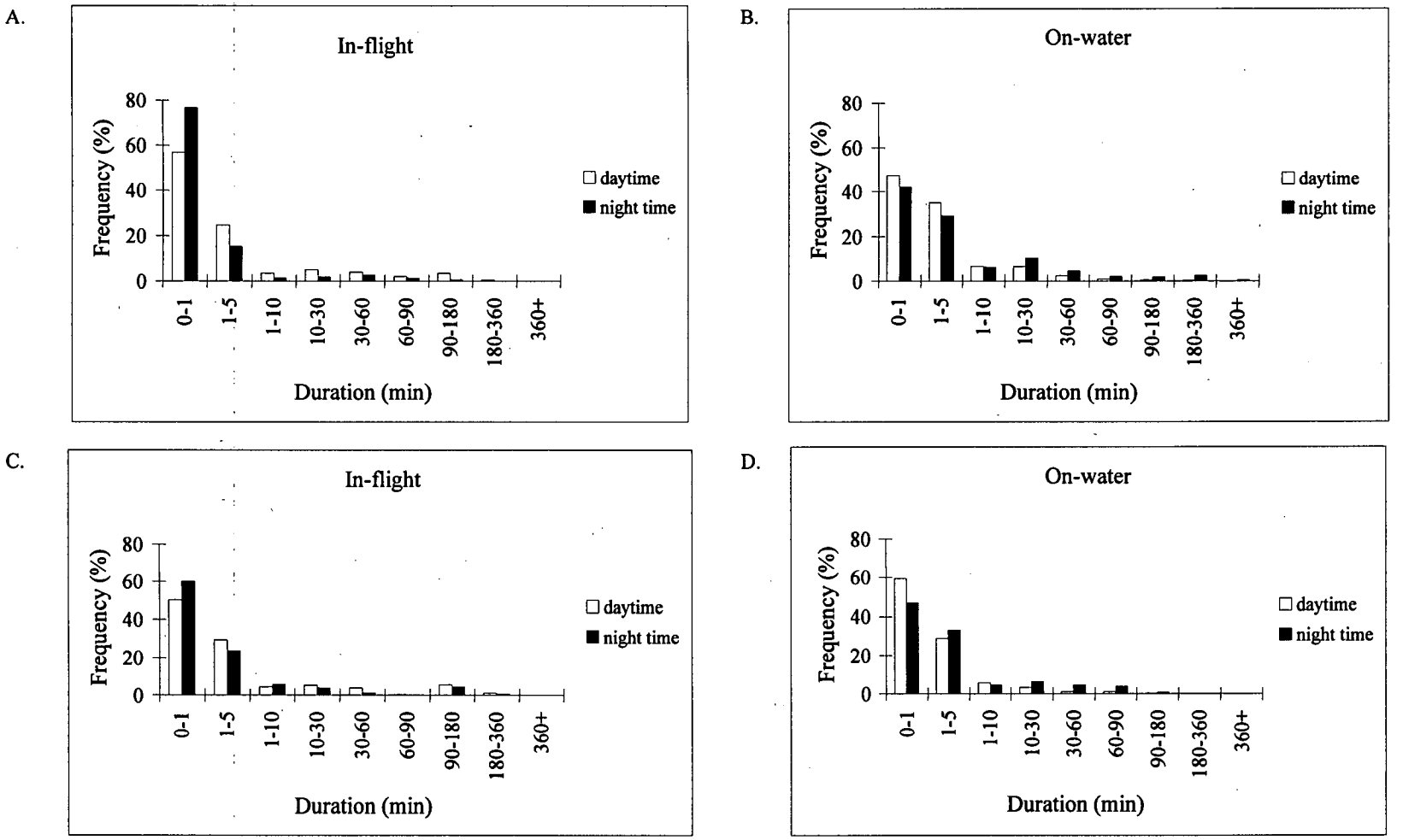


Figure 8.4. Distribution of the duration of in-flight and on-water bouts of Shy albatrosses during the day and night while foraging from Albatross Island during incubation (A and B) and brood (C and D) in 1996/97.

Similar to earlier findings (Brothers et al. 1998, and Chapter 3), all foraging by Shy albatrosses occurred over southeast Australian continental shelf and shelf slope waters. Birds foraged exclusively in the neritic zone, never crossing into oceanic pelagic waters.

8.3.6.1 *Albatross Island*

8.3.6.1.1 Incubation

When incubating, birds from Albatross Island mostly foraged between northwest Tasmania and southwest Victoria, generally on the western side of King Island, while some birds traveled west or southwest towards the edge of the continental shelf (Figure 8.5). Birds sit in rafts off Albatross Island bathing, and presumably resting, immediately after shift changes at the nest. These rafts occur throughout the season, but are most prevalent during incubation and chick-brooding (pers. obs.) At the fine scale (0.05 x 0.05° grids), birds did not tend to return to the same location to feed from one trip to the next. Overlap between successive foraging trips for the four individuals studied in 1995/96 averaged just 14 ± 6.4%, and just 9 ± 5.8% for three individuals studied in 1996/97 (Table 8.6). The foraging locations of the albatrosses, however, were not random. Constant headings from the Island were maintained on successive foraging trips, this consistency being demonstrated by increased overlap scores at the broad scale; 45 ± 22.4% across individuals in 1995/96 and 32 ± 9.0% in 1996/97.

There was also an element of individual variability (Table 8.6). On three successive trips in 1996/97, Bird 10 revisited just 6 ± 2.0% of the foraging areas (at the fine scale, Figure 8.6a), whereas on two successive foraging trips in 1995/96, Bird 3 revisited 16 ± 12.9% of the same areas northwest of King Island (Figure 8.6b). At the broad scale, overlap for Bird 3 increased to 62%.

While most birds foraged northwest of Albatross Island during incubation, there was relatively little overlap in the foraging zones of different individuals, averaging from 8 ±5.7% overlap in 1993/94 to 18 ± 6.2% in 1996/97 at the fine scale (Table 8.6). At the broad scale overlap figures ranged between 26 ± 17.9% and 49 ± 10.1%. The foraging zones of the three birds studied in 1996/97 are depicted in Figure 8.7.

At the population level, the foraging zones were highly consistent from one year to the next (Figure 8.5). Even at the fine scale, the foraging zones overlapped by 37 ± 7.9%, increasing to 65 ± 8.8 % at the broad scale.

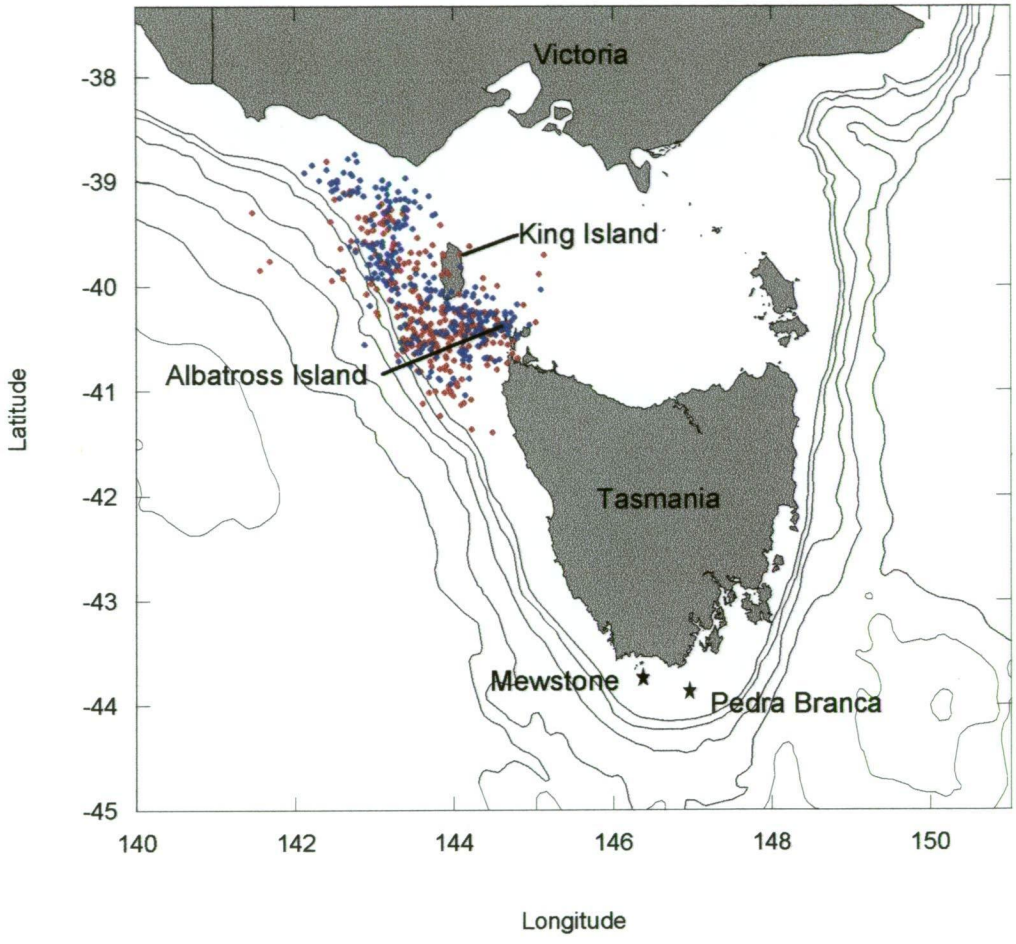


Figure 8.5. At sea locations of Shy albatrosses foraging from Albatross Island during the incubation stage in 1995/96 (red) and 1996/97 (blue).

Table 8.6: Percentage overlap in the foraging zones of Shy albatrosses from Albatross Island during the incubation stage in 3 breeding seasons (1993/94, 1995/96, and 1996/97).

Season	Level of analysis	Individual	No. of foraging trips or individuals	Fine scale (0.05° x 0.05° blocks) Foraging zone size Blocks used (mean ± SD)	Fine scale Foraging zone size Area (km²)	Fine scale % overlap (mean ± SD)	Broad scale (0.25° x 0.25° blocks) Foraging zone size Blocks used (mean ± SD)	Broad scale Foraging zone size Area (km²)	Broad scale % overlap (mean ± SD)
1993	*Ind	8 Inds	8 Inds	59 ± 31.0	1,410	8 ± 5.7%	11 ± 4.6	6,529	26 ± 17.9%
	*FT	Bird 1	5	62 ± 37.2	1,482	4 ± 3.7 %	11 ± 7.9	6,529	14 ± 13.7%
		Bird 2	3	34 ± 2.1	813	16 ± 8.1%	5 ± 1.0	2,968	61 ± 10.3%
		Bird 3	2	83 ± 16.3	1,984	16 ± 2.8%	13 ± 0.0	7,716	62 ± 0.0%
1995		Bird 4	5	44 ± 18.9	1,052	18 ± 9.8%	9 ± 4.8	5,342	43 ± 32.7%
		FT Mean	**4 ± 1.5**	**49 ± 29.1**	**1,333**	**14 ± 6.4%**	**10 ± 3.4**	**5,639**	**45 ± 22.4%**
	Ind	4 Inds	14 FTs	151 ± 59.3	3,610	15 ± 11.1 %	20 ± 9.5	11,872	46 ± 17.8%
	FT	Bird 1	3	48 ± 38.7	1,148	6 ± 1.6%	11 ± 4.2	6,529	23 ± 19.3%
		Bird 9	3	65 ± 4.7	1,554	16 ± 12.9%	12 ± 2.0	7,122	41 ± 35.2%
1996		Bird 10	3	52 ± 24.2	1,243	6 ± 2.0%	10 ± 4.9	5,935	33 ± 15.6%
		FT Mean	**3**	**55 ± 8.9**	**1,315**	**9 ± 5.8%**	**11 ± 1.0**	**6,529**	**32 ± 9.0%**
	Ind	3 Inds	9 FTs	185 ± 17.2	4,423	18 ± 6.2%	21 ± 1.2	12,464	49 ± 10.1%
1993		12 Inds	12 Inds	359	8,583		42	24,928	
1995 &	*Popn	31 FTs	31 FTs	459	10,974	37 ± 7.9%	41	24,335	65 ± 8.8%
1996				330	7,890		32	18,993	

*FT = successive foraging trips of an individual bird
*Ind = comparison of the foraging zones of indivdual birds studied contemporaneously (with all successive foraging trips of each individual combined)
*Popn= "population" level seasonal comparisons (with data for all individuals combined)

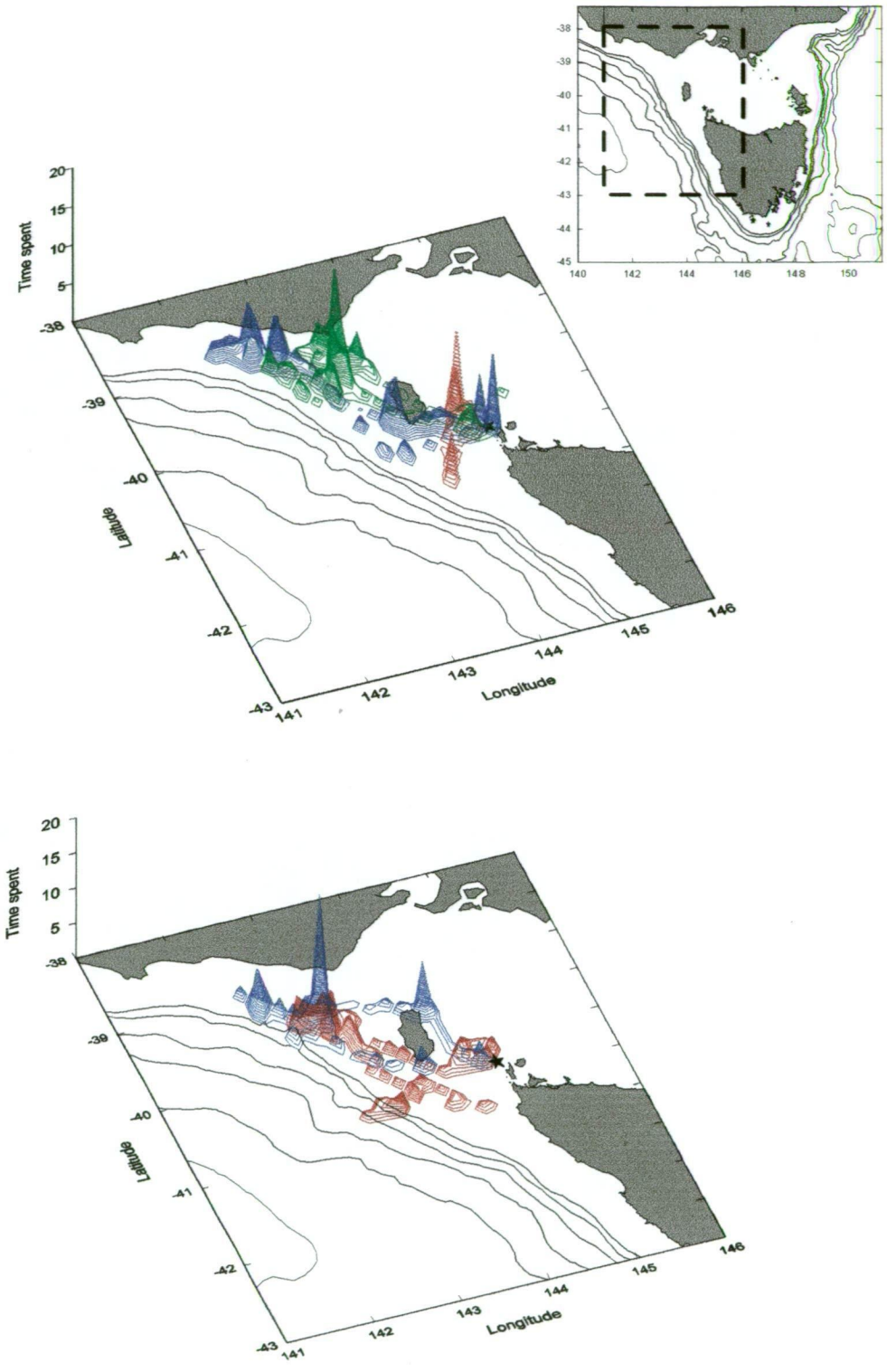


Figure 8.6. Successive foraging tracks of birds from Albatross Island during incubation, (A) three successive foraging trips of Bird 10 1996/97, and (B) two successive trips of Bird 3 during 1995/96. The Z-axis represents the number of 10 minute periods the albatrosses spent in each 0.05 degree grid square.

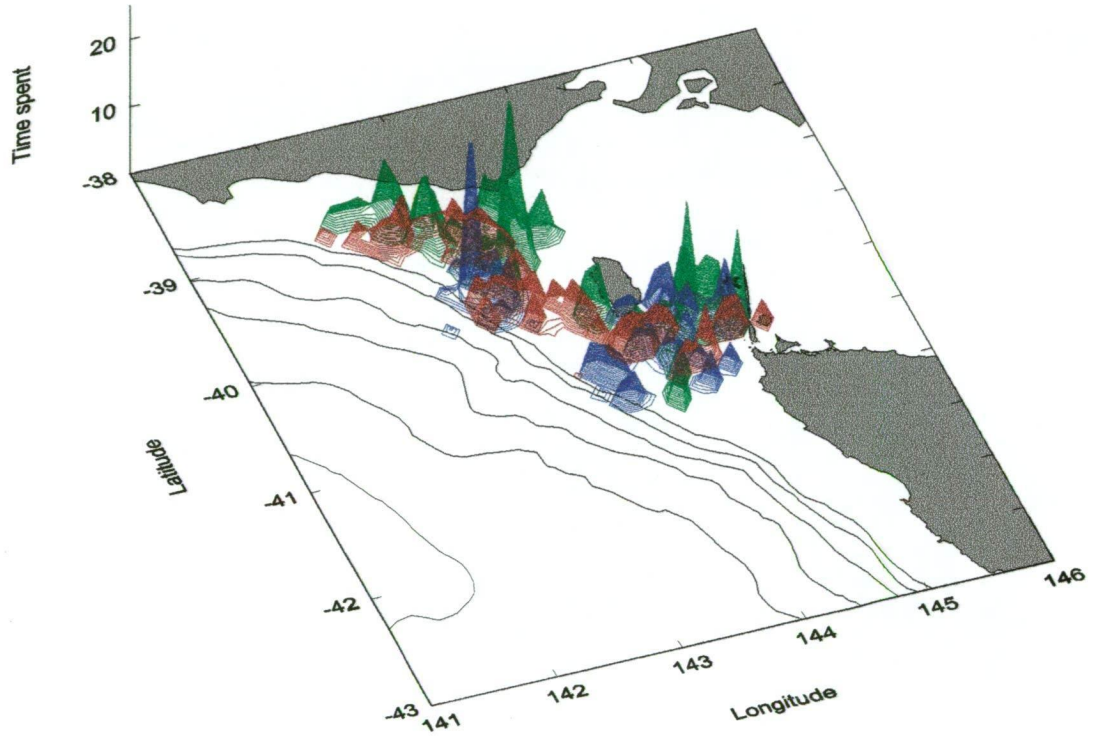


Figure 8.7. Depiction of overlap in the foraging zones (ie, grid squares where birds spent more than the median amount of time while at sea) of the three individual Shy albatrosses studied during incubation 1996/97 at Albatross Island. Bird 1 (red), Bird 9(blue), Bird 10 (green).

8.3.6.1.2 Chick-brooding

There is an overall contraction and spatial shift in the foraging zones of birds from Albatross Island between incubation and chick-brooding (Figure 8.8). When brooding chicks, birds forage within 100 km of the colony, and they return to the colony each day to swap duties at the nest. Brooding birds forage both east of King Island and directly south of Albatross Island, areas that are not heavily used during the incubation stage. Also when brooding chicks adults do not forage further north than King Island.

On almost all successive foraging trips birds maintained a constant heading from Albatross Island, however, similar to during incubation, the exact foraging locations differed from one trip to the next. At the fine scale, overlaps averaged just 10 ± 4.0% for six individuals in 1995/96 and 15 ± 8.1% for 10 individuals in 1996/97 (Table 8.7). While there was still some degree of individual variability, birds were more likely than not to repeatedly work the same patches of water on successive trips to sea. At the broad scale, foraging zones overlapped by 35 ± 15.6% in 1995/96 and 43 ± 15.8% in 1996/97. For example, in 1995/96 Bird 1 headed directly west of Albatross Island on 13 successive foraging trips, whereas, in the same year, Bird 8 headed north of Albatross Island to forage exclusively east of King Island. To maintain clarity, just three trips of Bird 8 (1995/96) and Bird 18 (1996/97) are provided in Figures 8.9a and 8.9b, respectively. The degree of overlap between successive foraging trips was similar during all stages of the breeding season, at the fine and broad scales ($F_{2,19}$=0.03, $p > 0.05$, $F_{2,19}$=0.09, $p > 0.05$).

The foraging zones of contemporaneously studied individuals overlapped somewhat less during chick-brood than during incubation (average 27 versus 40% across years), but this difference was not statistically significant at either the fine or broad scales ($F_{1,4}$=0.12, $p > 0.05$, $F_{1,4}$=2.16, $p > 0.05$). Figure 8.10 depicts the foraging zones of three Birds (14, 16 and 17) during chick-brood in 1996/97. Bird 16 fed east of King Island on three of four foraging trips, while for four successive trips each Birds 16 and 17 fed due west of Albatross Island between the colony and the edge of the continental shelf.

Overlap in the foraging zones of males and females was assessed during the brooding period. Paired t-tests indicated that the foraging zones of breeding pairs overlapped by an extent similar to all other individuals studied concurrently, (t=-0.18, df=3 and p=0.88), but to no greater degree. Overlap in foraging zone use by males and females was high, and ranged between 33 ± 12.0% and 53 ± 21.4% in 1995/96 and 1996/97 at the fine scale, and between 54 ± 32.2% and 70 ± 42.4% at the broad scale. At least during this stage of

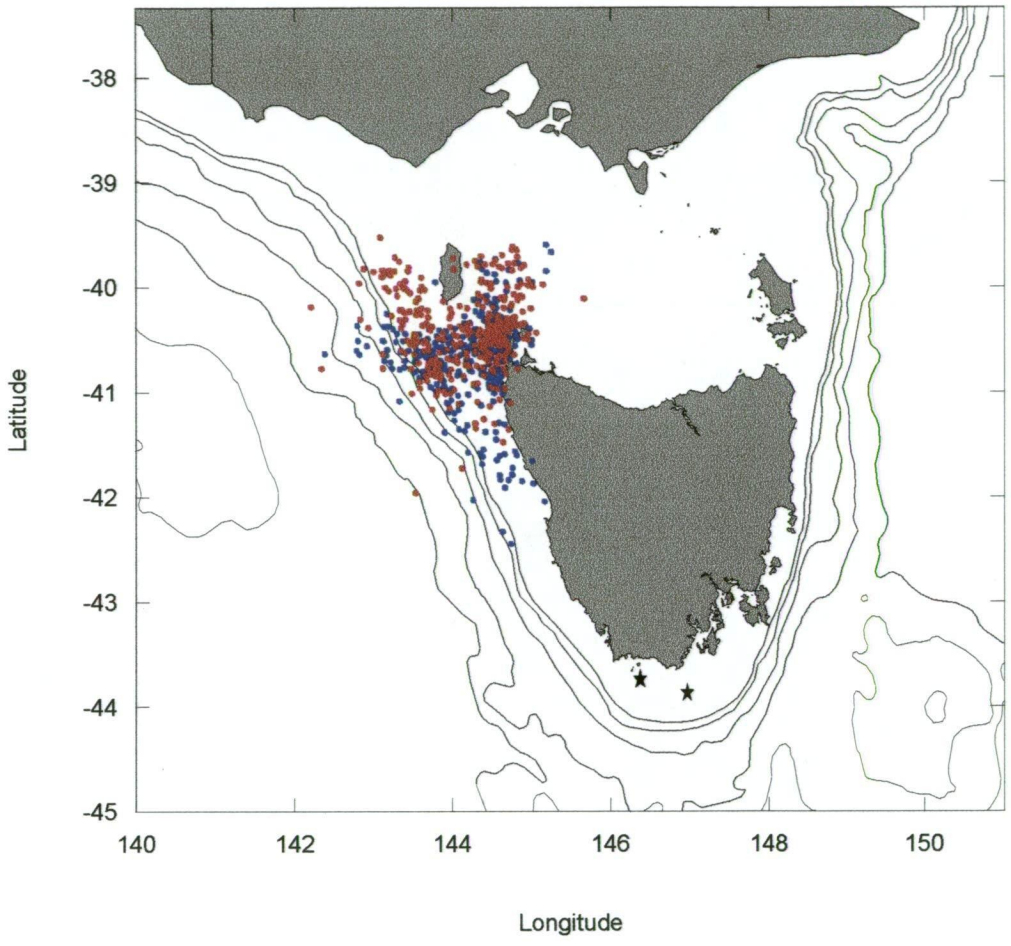


Figure 8.8. At sea locations of Shy albatrosses foraging from Albatross Island during the chick-brooding stage in 1995/96 (red) and 1996/97 (blue).

Table 8.7: Percentage overlap in the foraging zones of Shy albatrosses from Albatross Island during the chick-brooding stage in three breeding seasons (1993/94, 1995/96, and 1996/97). Foraging zone overlap and abbreviations are as in Table 8.6.

Season	Level of analysis	Individual	No. of FTs or Ind's involved	Fine scale (0.05° x 0.05° blocks) Foraging zone size Blocks used (mean ± SD)	Area (km^2)	% overlap (mean ± SD)	Broad scale (0.25° x 0.25° blocks) Foraging zone size Blocks used (mean ± SD)	Area (km^2)	% overlap (mean ± SD)
1993	Ind	16 Inds	16 Inds	42 ± 42.6	1,004	8 ± 9.0%	7 ± 4.4	4,155	22 ± 22.0%
	FT	Bird 1	10	13 ± 4.2	311	16 ± 17.6%	3 ± 2.0	1,781	62 ± 34.2%
		Bird 2	5	18 ± 13.0	430	6 ± 2.2%	5 ± 1.5	2,968	23 ± 25.9%
		Bird 5	3	28 ± 4.0	669	14 ± 2.0%	4 ± 0.6	2,374	23 ± 2.4%
1995		Bird 6	6	17 ± 11.1	406	7 ± 3.1%	6 ± 2.5	3,561	28 ± 15.0%
		Bird 7	8	28 ± 6.28	669	8 ± 4.8%	5 ± 2.3	2,968	27 ± 17.8%
		Bird 8	4	24 ± 12.7	574	10 ± 15.7%	5 ± 0.6	2,968	44 ± 19.9%
		FT Mean	**6 ± 2.9**	**21 ± 6.3**	**510 ± 149.3**	**10 ± 4.0%**	**5 ± 1.0**	**2,770 ± 612.9**	**35 ± 15.6%**
	Ind	6 Inds	6 Inds	104 ± 43.1	2,486	18 ± 9.8%	9 ± 5.5	5,342	34 ± 23.5%
	FT	Bird 5	5	15 ± 12.0	359	29 ± 13.7%	6 ± 2.6	3,561	28 ± 35.9%
		Bird 6	4	22 ± 11.5	526	5 ± 6.3%	5 ± 3.3	2,968	47 ± 27.8%
		Bird 12	6	22 ± 7.7	526	18 ± 11.0%	5 ± 2.7	2,968	30 ± 32.9%
		Bird 13	4	18 ± 14.9	430	16 ± 7.3%	4 ± 2.1	2,374	47 ± 18.4%
1996		Bird 14	3	24 ± 3.8	574	4 ± 5.2%	6 ± 1.0	3,561	43 ± 4.7%
		Bird 15	5	20 ± 15.7	478	17 ± 17.3%	4 ± 2.2	2,374	61 ± 27.7%
		Bird 16	4	18 ± 2.6	430	14 ± 4.0%	4 ± 2.6	2,374	53 ± 26.7%
		Bird 17	4	33 ± 15.5	789	15 ± 11.2%	5 ± 1.0	2,968	31 ± 10.1%
		Bird 18	4	25 ± 7.0	598	24 ± 14.3%	4 ± 1.4	2,374	69 ± 27.3%
		Bird 19	5	37 ± 20.6	884	6 ± 1.8%	7 ± 1.9	4,155	19 ± 11.6%
		FT Mean	**4 ± 0.9**	**23 ± 6.9**	**559 ± 164.1**	**15 ± 8.1%**	**4 ± 1.7**	**2,968 ± 625.7**	**43 ± 15.8%**
	Ind	10 Ind's	10 Ind's	80 ± 24.1	1,912	20 ± 9.6%	13 ± 4.7	7,716	37 ± 19.6%
1993	Popn	30 Inds	30 Inds						
1995 & 1996		100 FTs	100 FTs	416 ± 52.4	9,942	43 ± 9.9%	45 ± 9.1	26,709	61 ± 10.7%

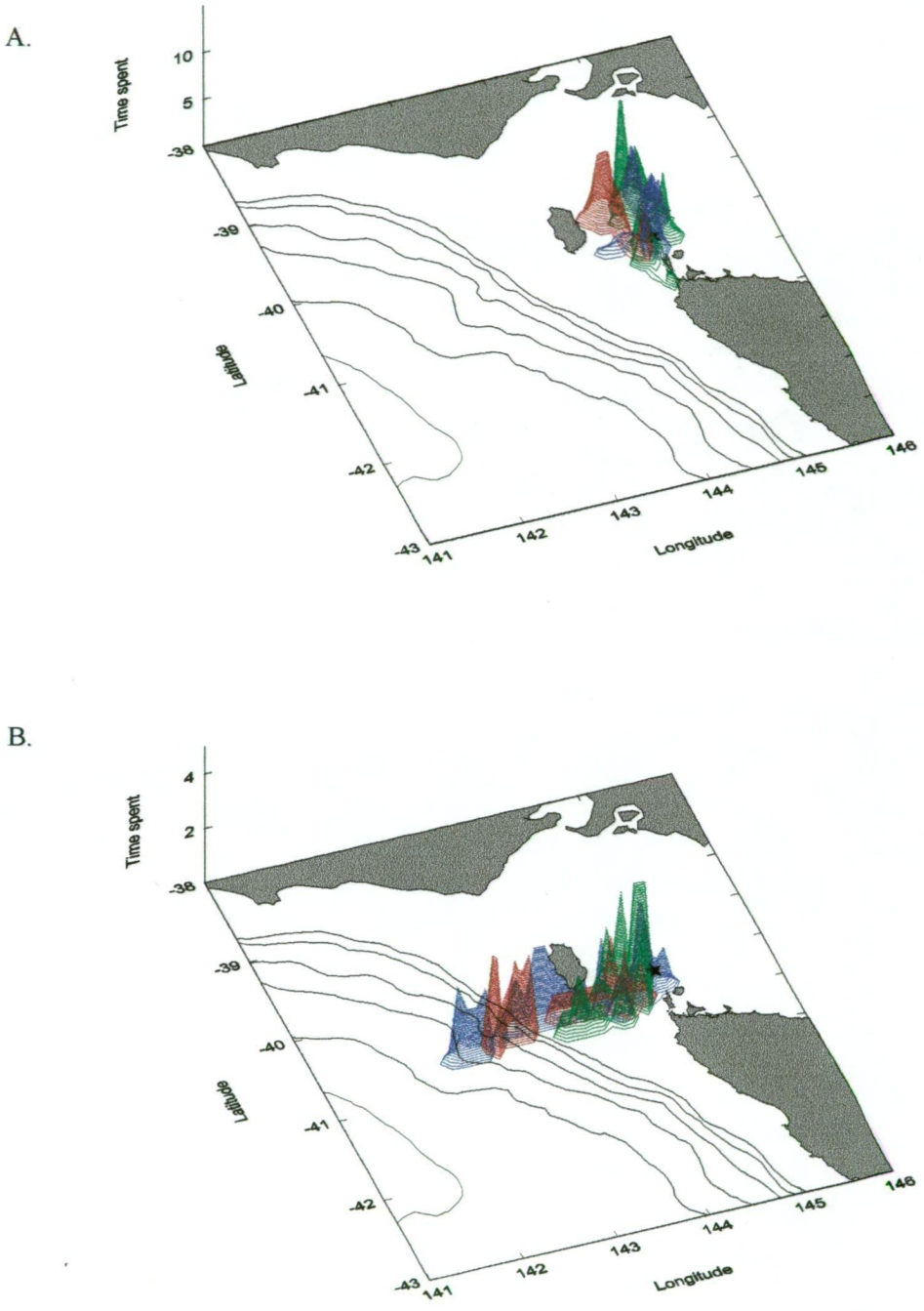


Figure 8.9. Successive foraging tracks of birds from Albatross Island during chick-brood. (A) Three successive foraging trips of Bird 8 in 1995/96, and (B) three successive trips of Bird 17 in 1996/97.

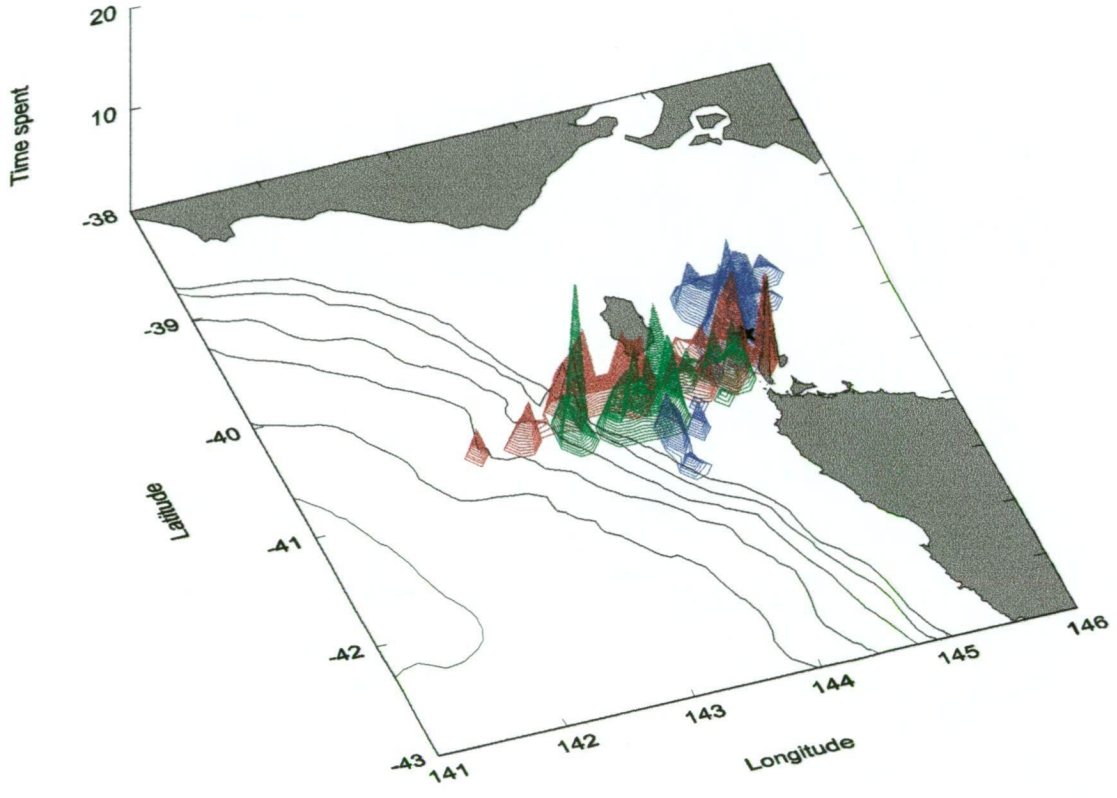


Figure 8.10. Depiction of overlap in the foraging zones (ie, grid squares where birds spent more than the median amount of time while at sea) for the three individual Shy albatrosses studied during chick-brood 1996/97 at Albatross Island. Bird 17 (red), Bird 16 (blue), Bird 14 (green).

the breeding season, then, there was no segregation of foraging zones between the sexes.

At the population level, the foraging zones used during chick-brooding were highly consistent between years, overlapping by 43 ± 9.9% at the fine scale and 61 ± 10.7% at the broad scale. While during 1993/94 and 1995/96 the foraging zones were almost identical, there was a southerly shift in 1996/97, with birds feeding west-southwest of Albatross Island, not using areas west of King Island as they had in the previous years.

8.3.6.1.3 Early chick-rearing

While the characteristics of foraging trips during early chick-rearing were intermediate between those during incubation and chick-brood, the birds headed west or southwest from Albatross Island to feed between the colony and the edge of the continental shelf, the area previously used during the brooding period. The foraging location varied on just one of the males 15 trips, when he headed south from Albatross Island to forage down Tasmania's west coast. On all other trips, the male and the female foraged in much the same area (Figure 8.11). Areas used on successive foraging trips overlapped by 12 ± 7.0% for Bird 21 and 14 ± 14.9% for Bird 20, at the fine scale, and by 39 ± 25.1% and 35 ± 20.2% at the broad scale (Table 8.8). Again while the heading was maintained, the exact foraging location differed somewhat between trips. The foraging zone of the male and female overlapped by 51 ± 23.8% at the fine scale and 61 ± 17.9% at the broad scale.

Table 8.8: Percentage overlap in the foraging zones of Shy albatrosses from Albatross Island during post-brood chick-rearing in 1996/97.

Season	Level of analysis	Bird (no. trips)	Fine scale (0.05° x 0.05° blocks) Foraging zone size			Broad scale (0.25° x 0.25° blocks) Foraging zone size		
			Blocks used (mean ± SD)	Area (km^2)	% overlap (mean ± SD)	Blocks used (mean ± SD)	Area (km^2)	% overlap (mean ± SD)
1996	FT	Bird 20 (15)	38 ± 24.6	909	14 ± 14.9%	7 ± 4.9	4,155	39 ± 25.1%
		Bird 21 (8)	34 ± 21.0	813	12 ± 7.0%	7 ± 3.3	4,155	35 ± 20.2%
	Ind	2 Inds	36 ± 2.0%	861	51 ± 23.8%	7 ± 0.0	4,155	61 ± 17.9%

8.3.6.1.4 Consistency in the foraging zones of individual birds between breeding stages and years

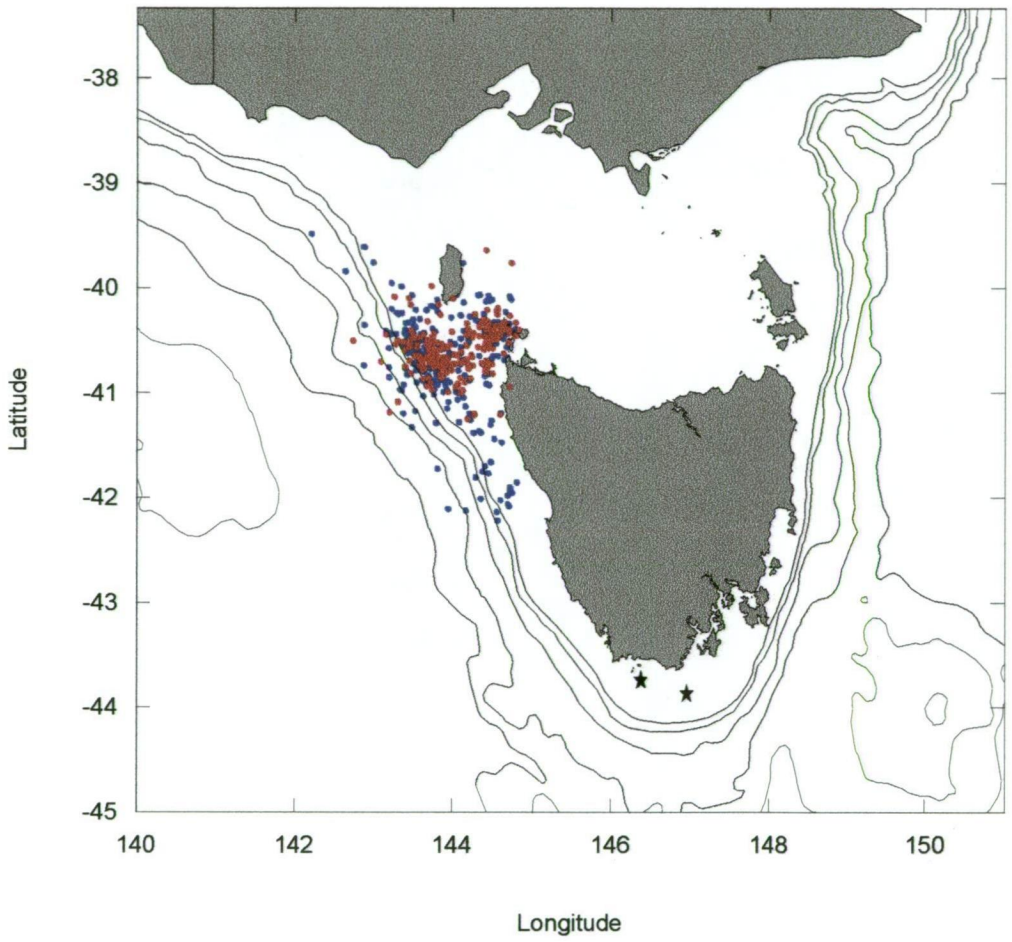


Figure 8.11. At sea locations of Shy albatrosses foraging from Albatross Island during early chick-rearing in 1996/97. Bird 21 (red) and Bird 20 (blue).

An area west-southwest from Albatross Island, along with the western side of King Island, was used by birds during both the incubation and chick-brooding periods. Overlap between these stages ranged from 21 ± 4.2% in 1993/94 to 46 ± 5.7% in 1995/96 at the fine scale and from 25 ± 4.3% in 1996/97 to 69 ± 3.7% in 1995/96 at the broad scale. Lower overlap scores in 1996/97 resulted from the southerly shift during the brooding period.

Five individual birds were satellite tracked two or more times between September 1993 and December 1996 (Birds 1,2,5,6 and 10), and overlap in the foraging zones used during these periods is given in Table 8.9. The overlap between breeding stages was similar to levels observed in the population as a whole. However, individual birds showed more flexibility in the locations of their foraging zones between years. For example, during incubation in both 1993/94 and 1996/97 Bird 10 foraged off the southwest coast of Victoria. In contrast, Bird 5, who was tracked during the brooding stage in 1993/94, 1995/96 and 1996/97 showed a lower degree of consistency, foraging down Tasmania's west coast during both 1995/96 and 1996/97, but exclusively east of King Island in 1993/94.

Table 8.9: Percentage overlap in the foraging zones of Shy albatrosses satellite tracked two or more times between September 1993 and December 1996 at Albatross Island. These sessions occurred either during two different stages of the same breeding season or during the same stage in two or more breeding seasons.

Individual	Tracking sessions	No. of foraging trips	Fine scale (0.05° x 0.05° blocks) % overlap (mean ± SD)	Broad scale (0.25° x 0.25° blocks) % overlap (mean ± SD)
Bird 1	Incubation 1995	5	(Incubation only)	(Incubation only)
	Brood 1995	10	13 ± 7.7%	46 ± 33.5%
	Incubation 1996	3	(Incubation & Brood 95)	(Incubation & Brood 95)
Bird 2	Incubation 1995	3	16 ± 1.0%	49 ± 18.9%
	Brood 1995	5		
	Brood 1993	2		
Bird 5	Brood 1995	3	11 ± 6.3%	24 ± 13.1%
	Brood 1996	5		
Bird 6	Brood 1995	6	19 ± 7.0%	47 ± 19.9%
	Brood 1996	4		
Bird 10	Incubation 1993	1	22 ± 11.9%	64 ± 20.2%
	Incubation 1996	3		

8.3.6.2 *Pedra Branca & Mewstone*

Breeding and post-breeding birds from both Pedra Branca and Mewstone foraged over

continental shelf and shelf slope waters south of Tasmania. Eighty-nine percent of the locations from Pedra Branca birds were obtained east of the Island (Figure 8.12a), while 79% of locations from Mewstone birds were obtained along Tasmania's west and southwest coasts, to the west of Mewstone.

8.3.6.2.1 Incubation at Pedra Branca

While incubating, Pedra Branca birds foraged east of the Island, as far north as Tasman Peninsula and to the south over continental shelf and slope waters. Successive foraging trips of individual birds overlapped by 19 ± 2.5% at the fine scale and by 49 ± 7.2% at the broad scale (Table 8.10). Figure 8.13 depicts the foraging zones of Bird 3 on three successive trips to sea. On the first and third trips this bird fed over the shelf southeast of Pedra Branca, while on the second trip foraging was focused just south of Tasman Peninsula. Overlap between individuals was somewhat higher at Pedra Branca than at Albatross Island, with birds using 38 ± 12.4% of the same foraging areas at the fine scale, and 61 ± 18.8% at the broad scale. The heightened degree of overlap likely results from the contracted foraging range of Pedra Branca birds, combined with the consistent use of an area south of Tasman Peninsula.

The foraging zones of the breeding pair overlapped by 7.9 ± 1.48%, and this was less than that observed for the population as a whole.

8.3.6.2.2 Overlap between breeding stages

During both early incubation in this study and during late incubation in 1994/95 (Brothers et al. 1998, and Chapter 3) foraging was concentrated mainly east of Pedra Branca. Overlap was consequently high; 54 ± 27.0% at the fine scale and 77 ± 33.2% at the broad scale. Using the broad scale, the foraging areas identified during late incubation 1994/95 were completely encompassed by areas used in early incubation 1997/98.

8.3.6.2.3 Chick-rearing at Mewstone

In stark contrast to the situation at Pedra Branca (just 43 km away), the birds from Mewstone foraged over the continental shelf almost exclusively west of the Island (Figure 8.12b). There was no clear change in foraging location through time, with much the same areas used from hatching through to fledging. The maximum foraging range was somewhat extended late in chick-rearing with one individual travelling as far north as the mid-west Tasmanian coast.

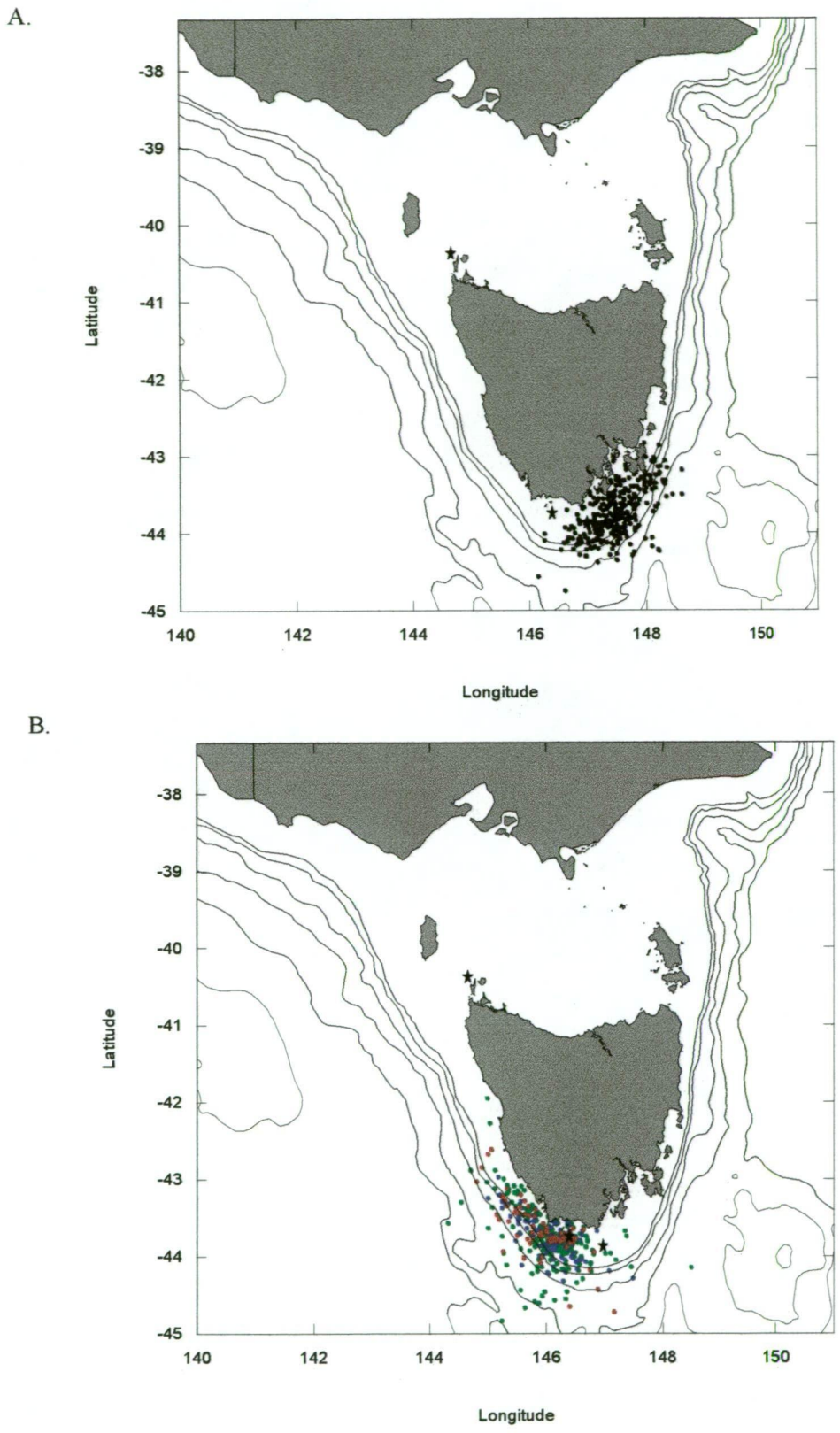


Figure 8.12. At sea locations of Shy albatrosses foraging from (A) Pedra Branca during incubation in 1997/98, and (B) from Mewstone during chick-brood (red), early chick-rearing (blue) and late chick-rearing (green) in 1997/98.

Table 8.10: Percentage overlap in the foraging zones of Shy albatrosses from Pedra Branca during incubation in 1997/98. Foraging zone overlap and abbreviations are as in Table 8.6.

Level of analysis	Individual	No. of FTs or Ind's involved	Fine scale (0.05° x 0.05° blocks) Foraging zone size Blocks used (mean ± SD)	Fine scale Foraging zone size Area (km^2)	Fine scale % overlap (mean ± SD)	Broad scale (0.25° x 0.25° blocks) Foraging zone size Blocks used (mean ± SD)	Broad scale Foraging zone size Area (km^2)	Broad scale % overlap (mean ± SD)
Ind	3 Inds	3 Inds	173 ± 73.0	3,910 ± 1,649.8	38 ± 12.4%	21 ± 7.8	11,866 ± 4,407.3	61 ± 18.8%
FT	Bird 1	6	44 ± 16.8	994 ± 379.7	17 ± 13.8%	9 ± 4.4	5,085 ± 2,486.2	45 ± 20.7%
	Bird 2	4	56 ± 21.0	1,266 ± 474.6	19 ± 8.7%	8 ± 2.6	4,520 ± 1,469.1	57 ± 20.7%
	Bird 3	4	30 ± 24.6	678 ± 556.0	22 ± 13.6%	5 ± 3.9	2,825 ± 2,203.7	44 ± 31.5%
	Mean	**5 ± 1.2**	**43 ± 13.0**	**972 ± 293.8**	**19 ± 2.5 %**	**7 ± 2.1**	**39,55 ± 1,186.6**	**49 ± 7.2%**

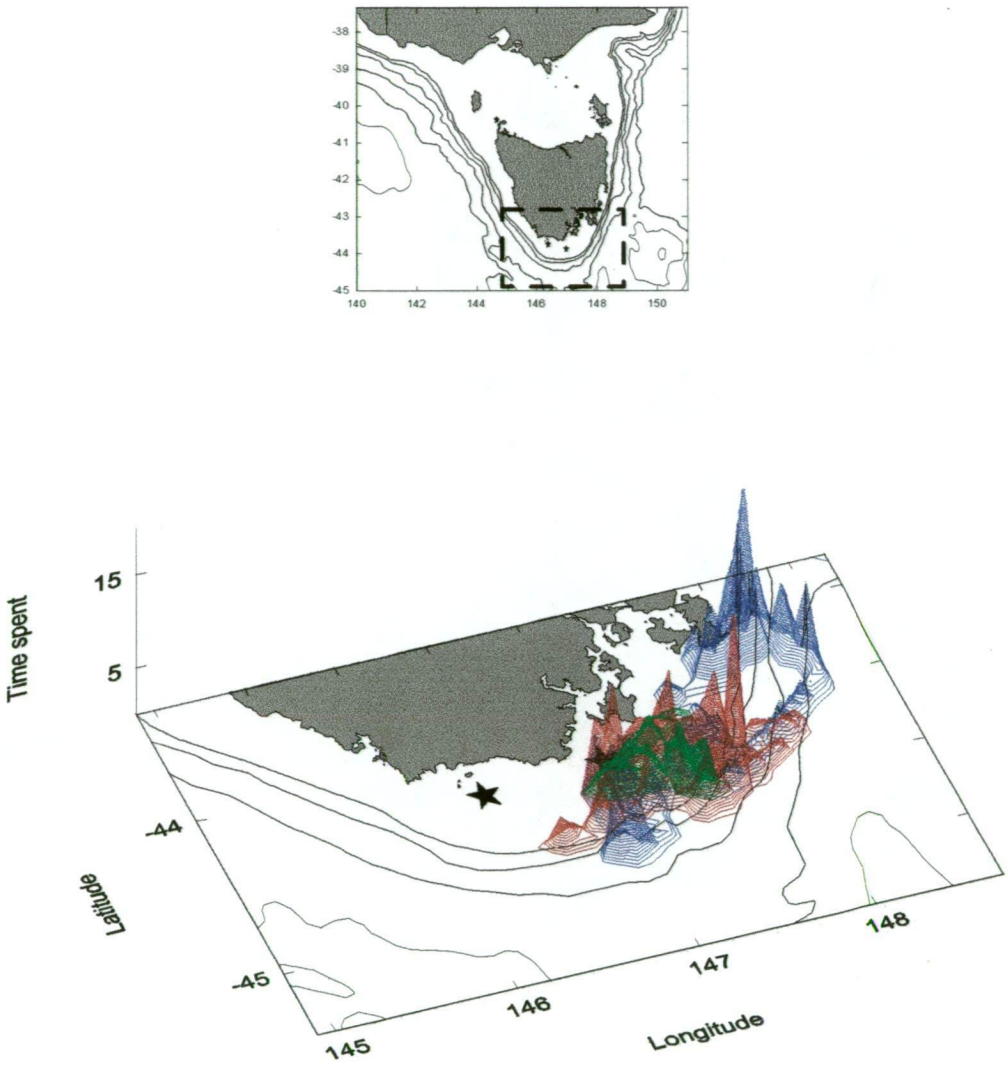


Figure 8.13. Successive foraging tracks of Bird 3 from Pedra Branca during incubation in 1997/98.

8.3.7 *Population level use of the foraging zones*

For each population, data were pooled across foraging trips to estimate the relative use of areas within the foraging zones (Figure 8.14). At both Albatross Island and Pedra Branca the greatest concentration of locations were obtained close to the Islands, however, other areas were also heavily used. At Albatross Island the area directly west of the island, between the colony and the shelf edge was an important foraging area, as was an area lying just south of King Island. Birds used these areas throughout the breeding season. Two areas also appeared particularly important for Pedra Branca birds. The birds heavily used an area over the shelf break east of the Island, and a second area that lay to the northeast in inner continental shelf waters. Note that areas at the extreme of the range, which tended to be used only during incubation, did not appear as important foraging areas overall.

8.3.8 *SST within the foraging zones*

The foraging locations of the albatrosses and contemporaneous SSTs during each tracking session from each population are shown in Figures 8.15a-c. Between incubation and early chick-rearing, birds from Albatross Island foraged in waters that ranged from 12 to approximately 17° C (Figure 8.15a). While there were substantial inter-annual variations in SST off Tasmania's east coast, especially during the 1997/98 El Niño event (Figure 8.15b), SSTs within the foraging zones of Albatross Island birds were highly consistent between years.

During the 1994/95 and 1997/98 breeding seasons, birds from Pedra Branca and Mewstone foraged in waters that ranging from 12 to approximately 16° C (Figure 8.15b). In the areas used by Pedra Branca birds, SSTs were similar between the 1994/95 and 1997/98 seasons (Figure 8.15b). During the 1997/98 study at Mewstone, there was little variation in the birds foraging areas from the beginning of the brooding period (December) until they fledged their chicks in April. This consistency was mirrored by the physical oceanography, as across the breeding season SSTs variations did not exceed 2° C (range 13-15 ° C). Despite considerable SST warming in both eastern Bass Strait and in coastal waters off northeast Tasmania, the 1997/98 El Niño appeared to have little influence on SST off Tasmania's south coast in areas where the albatrosses were foraging (Figure 8.15b).

Data collected during the post-breeding period (Brothers et al. 1998, and Chapter 3),

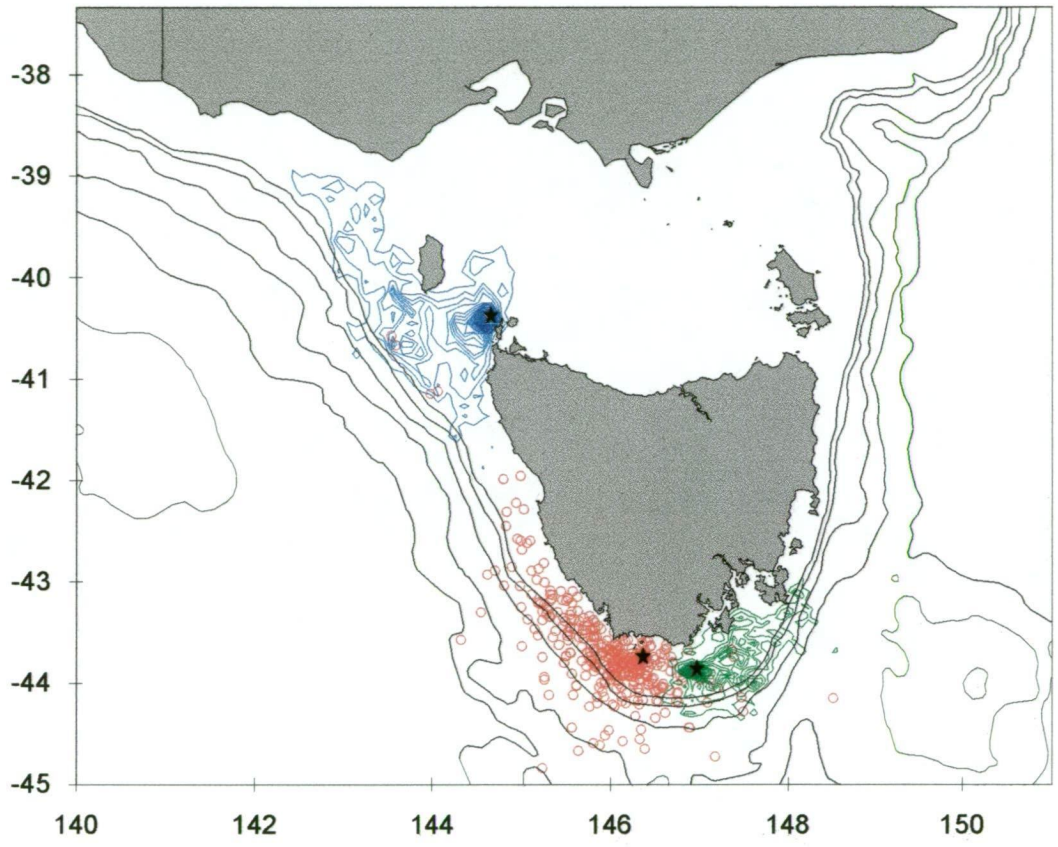


Figure 8.14 Population level use of areas within the foraging zones. Contours represent the relative proportion of at-sea time spent in each 0.05° grid square along the foraging routes. Data have been contoured at Albatross Island and Pedra Branca, and all locations received for birds foraging from Mewstone have been added for comparison.

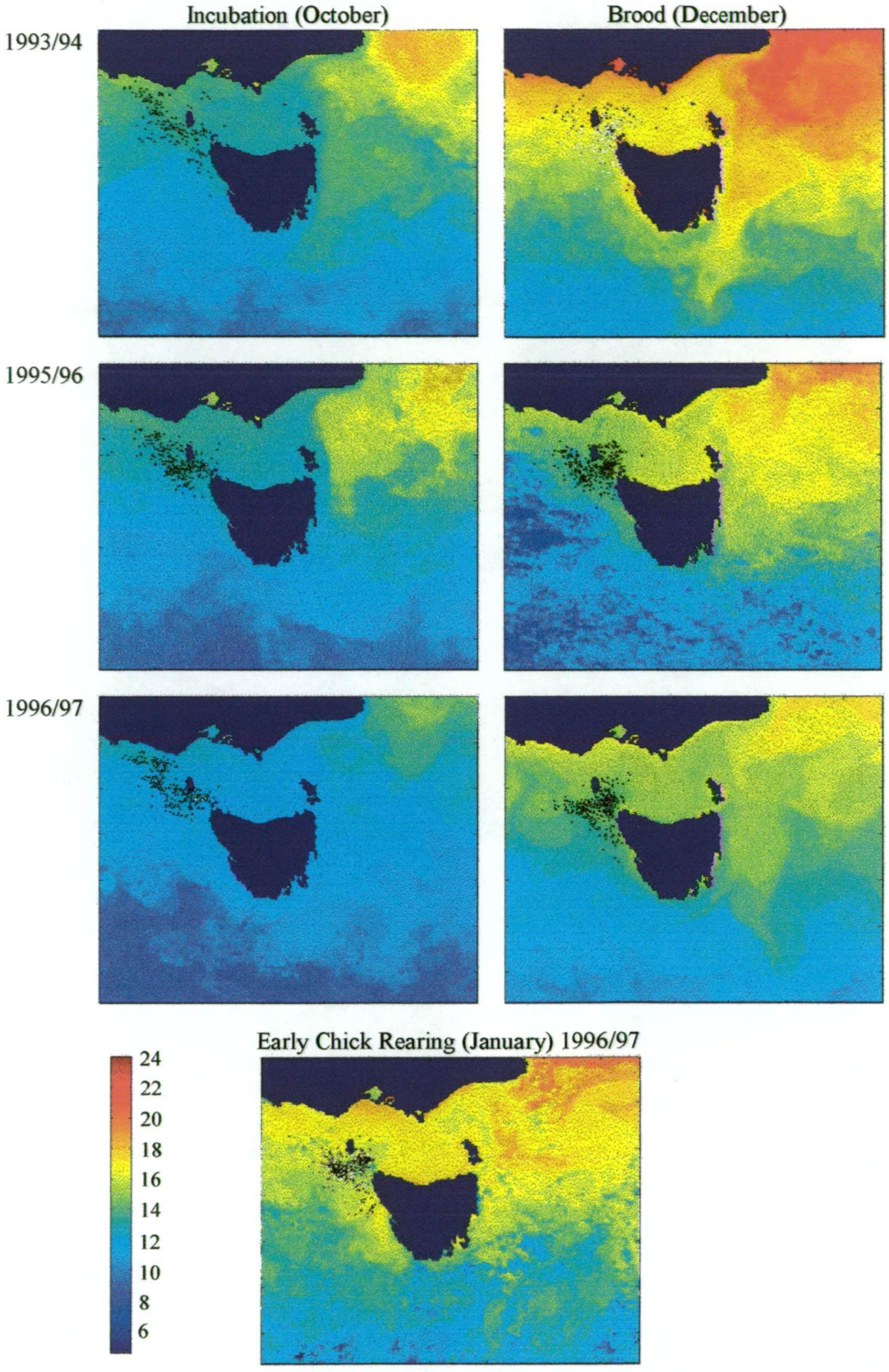


Figure 8.15A: Foraging locations of birds from Albatross Island overlaid upon Sea Surface Temperature (SST) plots during the incubation (left hand column) and brooding (right hand column) periods of the 1993/94, 1995/96 and 1996/97 breeding seasons. SSTs during early chick-rearing 1996/97 are depicted in the bottom figure. Images are weekly median filtered composites and temperatures (°C) are estimated for each 3.3 km x 3.3 km grid square.

Pedra Branca

Brood (December) 1994/95

Incubation (November) 1997/98

Mewstone

Brood (December) 1997/98

Early Chick-rearing (January) 1997/98

Late Chick-rearing (February/March) 1997/98

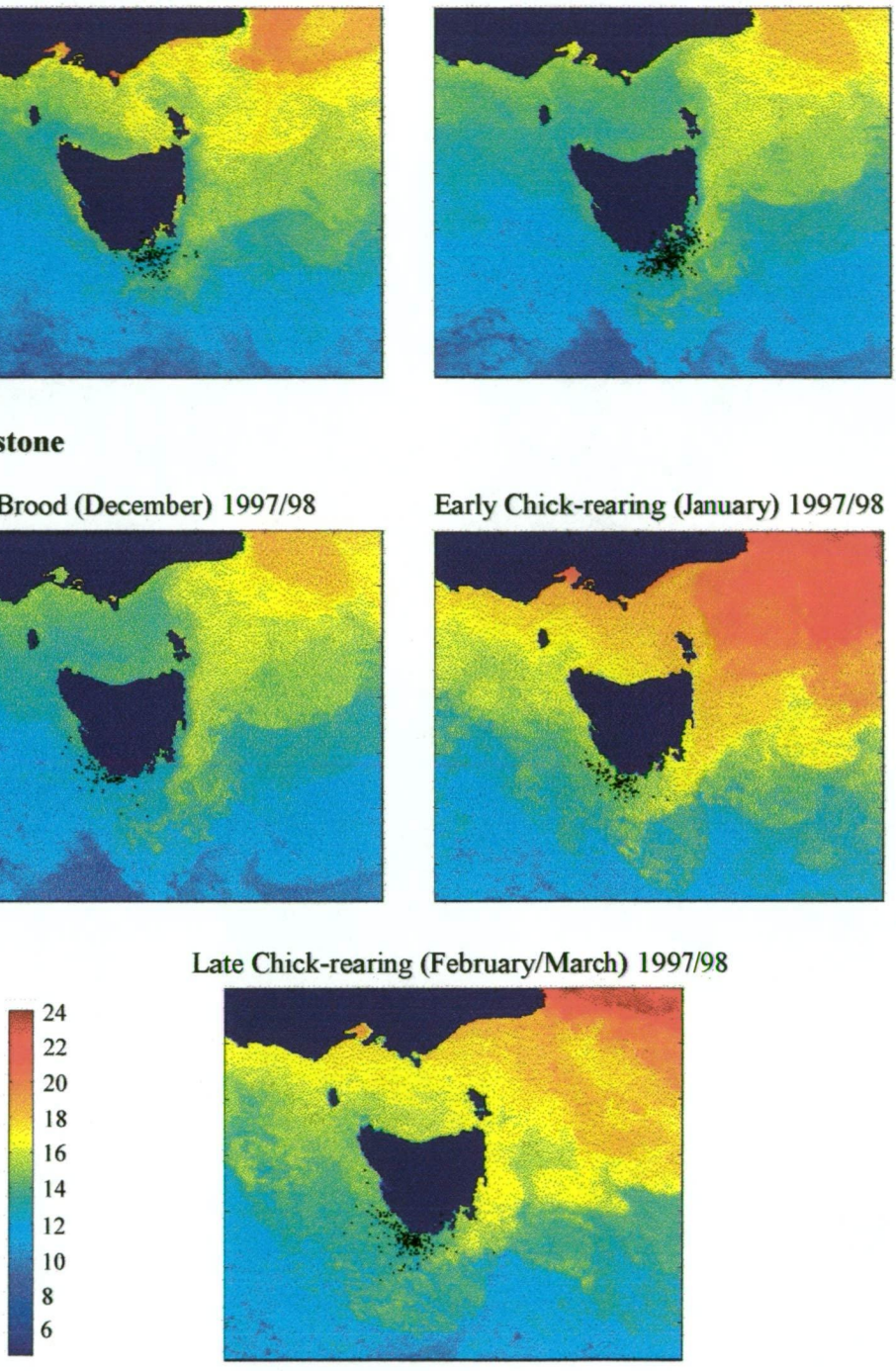


Figure 8.15B: Foraging locations of birds from Pedra Branca and Mewstone overlaid upon plots of Sea Surface Temperature. Tracking dates are indicated and particulars of the images are as in Figure 8.15A.

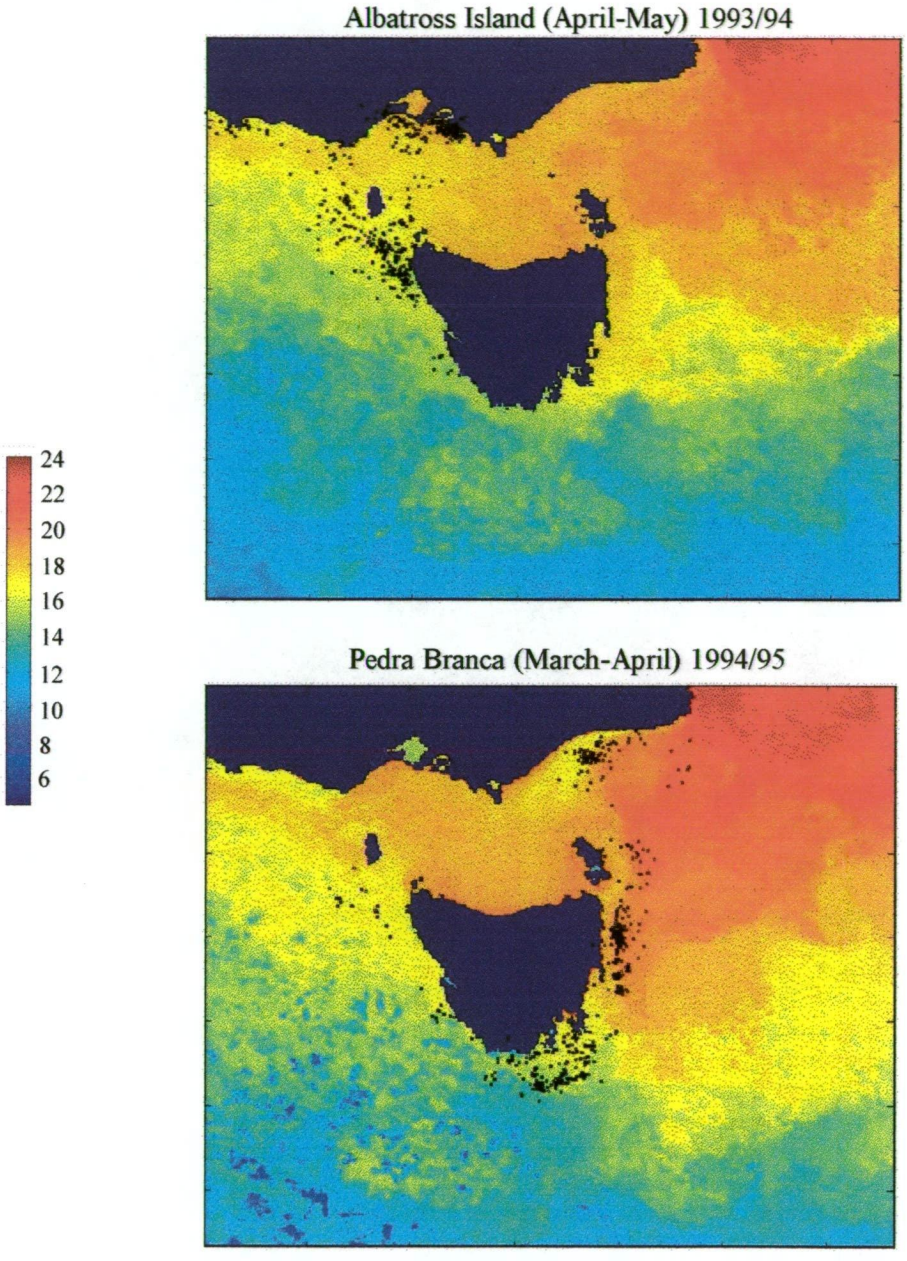


Figure 8.15C: Foraging locations of post-breeding birds from Albatross Island and Pedra Branca overlaid upon plots of Sea Surface Temperature. Tracking dates are indicated and particulars of the images are as in Figure 8.15A.

covered April and May of the 1993/94 season from Albatross Island, and March and April of the 1994/95 season from Pedra Branca. Pedra Branca birds clearly foraged in upwelling areas associated with the continental shelf break off both the east coast of Tasmania and the southeast coast of Victoria (Figure 8.15c). SSTs in these areas varied from approximately 16 to in excess of 20° C (Figure 8.15c). Birds from Albatross Island made wider use of inner shelf areas off northwest Tasmania and southwest Victoria where SSTs ranged from 16 to approximately 18° C (Figure 8.15c).

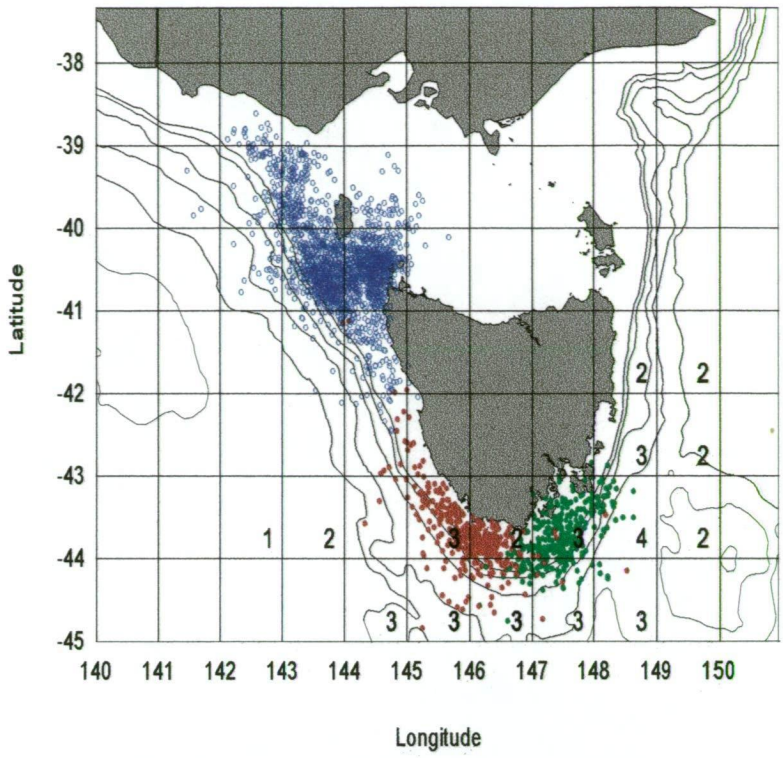
8.3.9 *Interactions with longline fisheries*

The former Japanese and ongoing Australian domestic longline fisheries concentrate their efforts off the south, east and west coasts of Tasmania. During 1995 the Japanese fished almost year round (January to October), while in 1996 and 1997 fishing was limited to the winter months (June to October in both years). Australian domestic longlining occurred throughout the year from 1995 to 1997, but much of the effort was concentrated in summer (AFMA data base).

There would have been minimal overlap between birds from Albatross Island and the Japanese or Australian domestic longline fisheries between 1995/96 and 1997/98. No hooks were set by Australian domestic fishers in areas used by breeding Shy albatrosses from this site, and hooks were set by the Japanese off the west coast in just one of the 18 1° grid squares known to be used by the birds (Figure 8.16a). Similarly, at least within the AFZ, no hooks were set by either fishery in areas known to be used by Albatross Island birds outside the breeding season (Brothers et al. 1998, and Chapter 3, Figure 8.16b).

Birds breeding at Pedra Branca and Mewstone, however, would have overlapped extensively with both the Japanese and Australian domestic longline fisheries during their breeding and post-breeding periods. Between 1995/96 and 1997/98, hooks were set by the Japanese in 75% (6 of 8 grid squares) of areas, and by the Australian domestic fleet in 88% (7 of 8 grid squares) of areas known to be used by breeding birds from Pedra Branca (Figure 8.16a). Hooks were set respectively by these fisheries in 36% (9 of 25 grid squares) and 16% (4 of 25 grid squares) of areas known to be used by post-breeding birds from this site (Figure 8.16b). Interactions would have occurred off Tasmania's south and east coasts. Between 1995/96 and 1997/98 hooks were set off the west and south coasts of Tasmania by both Japanese and Australian domestic fisheries in 67% (8 of 12 grid squares) of areas used by Mewstone birds when raising chicks (Figure 8.16a). Data were

A.



B.

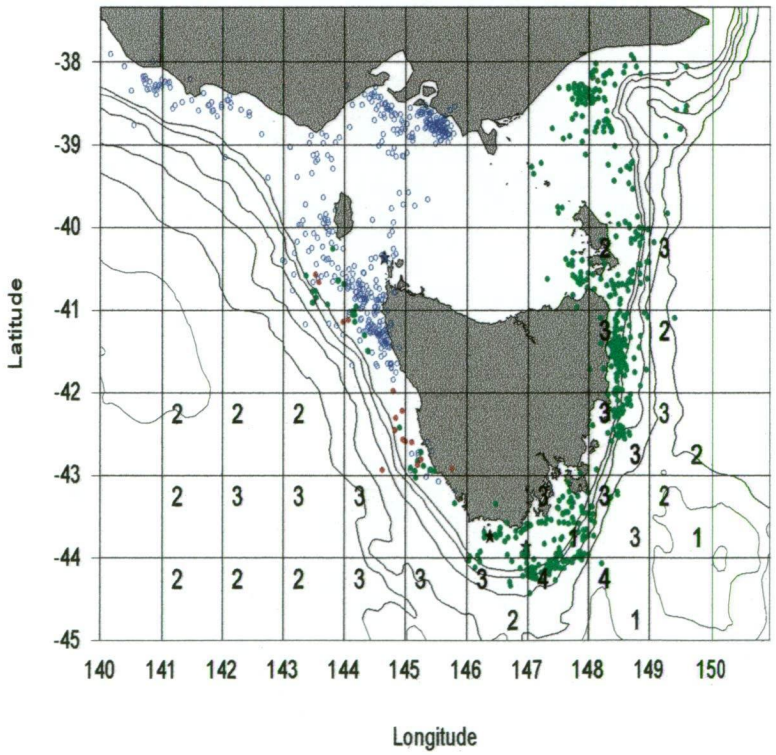


Figure 8.16. Overlap of Albatross Island (blue), Pedra Branca (green) and Mewstone (red) Shy albatrosses with Japanese (upper left-hand corner) and Australian domestic (lower right-hand corner) longline fisheries during (A) the breeding (September to April) and (B) the non-breeding periods (May-August) from 1995/96 to 1997/98. Fishing effort is depicted as the total number of hooks set in each 1 ° x 1 ° block as follows: 1= 1 to 999, 2=1000 to 9,999, 3=10,000 to 99,999, 4= 100,000 to 999,999.

not collected to allow assessment of potential interactions between Mewstone birds and fisheries outside the breeding season.

8.3.10 *Influence of fishing vessels on the at-sea distribution of Shy albatrosses*

As most information was gathered from Albatross Island, discussion of the potential influence of fishing vessels on the at-sea distribution of Shy albatrosses will be limited to this site. An immense amount of fishing occurs within the foraging zone of Albatross Island birds (Figure 8.17), both during their breeding and non-breeding periods. However, given the characteristically large quantities of discards and by-catch, the Southeast trawl fishery would potentially have the largest influence on albatross distribution at sea. Contemporaneous overlap between the albatrosses and the distribution of effort in the Southeast trawl, the Rock lobster and the Tasmanian Finfish fisheries are provided in Figure 8.17. Effort in the Trawl fishery is depicted in the upper left-hand corner, that for Rock Lobster in the middle, and that for the Finfisheries in the bottom right-hand corner of each square. Trawling occurs along the continental shelf and slope (Figure 8.17), with the most intensive effort expended directly west and south of Albatross Island, as well as further north off the south coast of Victoria. Overlap between the trawl fishery and the albatrosses ranged from 11% (2 of 18 grid squares) during the nonbreeding period to 44% (4 of 9 grid squares) during chick-rearing. When examined simply as vessel presence or absence, trawling consistently occurred in more than 50% of areas also used by the albatrosses. The spatial nature of effort in the Trawl fishery is relatively constant from incubation to early chick-rearing, and at least within the past five years it has been relatively constant per year.

Rock lobsters inhabit shallow reefs in waters to 150 m, and as a result, the fishery is limited to waters over the continental shelf (S. Frusher, pers. comm.). The fishery commences in November each year and continues through to August. Effort is substantial in inshore waters directly north, west and south of Albatross Island (Figure 8.17). Overlap between the albatrosses and this fishery was high, with Rock lobster fishing occurring in 33% (6 of 18 grid squares) of the birds foraging areas during the non-breeding period, and as much as 78% (7 of 9 grid squares) of the foraging areas during chick-rearing. Because of its smaller size, the Tasmanian Finfish fishery was considered to have the least potential influence, however, proportionately it has amongst the highest overlap with foraging albatrosses. Effort is substantial in areas around Albatross Island throughout the breeding season, and in the years for which we have data, fishing occurred in between 64% (9 of 14 grid squares during incubation) and 78% (7 of 9 grid squares

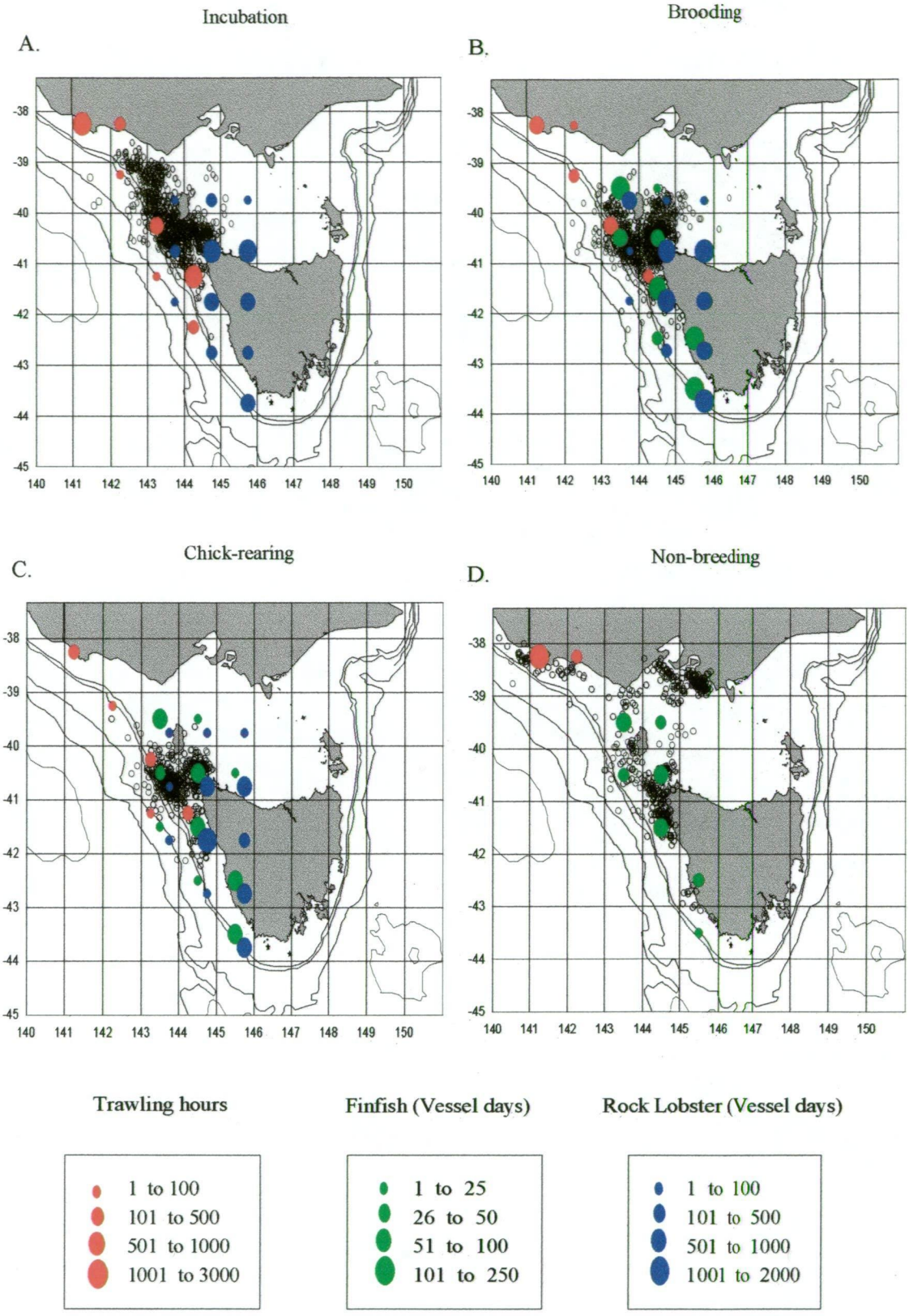


Figure 8.17. Distribution at-sea of Shy albatrosses from Albatross Island relative to the distribution of effort in the Southeast Trawl (Red, upper left hand corner), the Southern Rock lobster (Green, middle), and the Tasmanian Finfish fishery (Blue, bottom left hand corner) in each grid square during (A) the incubation period, (B) the chick-brooding period, (C) the early chick-rearing period, and (D) the non-breeding period.

used during chick-rearing) of areas also used by the birds (Figure 8.17).

8.4 DISCUSSION

This multi-year study reports on the at-sea distribution of the three Shy albatross populations in Tasmania. Unique amongst albatrosses studied to date, Shy albatrosses are relatively sedentary both during and outside the breeding season (Brothers et al. 1997, 1998, and Chapter 3). While breeding, birds from all sites spend short periods at sea (generally less than 3 days), and they forage exclusively over continental shelf waters close to their colonies. The maximum foraging range at all sites averaged less than 200 km (180 km at Albatross Island during incubation, 88 and 176 km at Pedra Branca and Mewstone during incubation and late chick-rearing, respectively). Birds repeatedly concentrate their searching efforts over the same broad patches of water on successive foraging trips, however, the particular locations visited within the zones may change from one trip to the next. At the population level, foraging zones are highly consistent between years. Despite the relative proximity of the colonies, especially Pedra Branca and Mewstone (which lie just 43 km apart), the three populations have mutually exclusive foraging zones during the breeding season. Consistency in the foraging locations between years, coupled with area-specific by-catch rates in longline fisheries (Gales et al. 1998), result in different likely impacts for birds breeding at the three sites.

8.4.1 *Effect of carrying satellite packs*

The longer foraging trip durations of birds carrying satellite packs as opposed to the lighter VHF transmitters indicated increased energetic costs associated with carrying heavier instruments (satellite packs 1.9-2.4% (Telonics) or 2.6-3.4% (Toyocom) vs VHF transmitters 0.4-0.5% adult body mass). While the methodology was somewhat different in each case, this was unlikely to have accounted for the significant differences in trip durations. Attendance cycles of birds carrying VHF transmitters were highly accurate, and electronically recorded within five minutes of the bird's actual arrival to or departure from the colony. While the attendance patterns of birds carrying satellite packs were less accurate (being reliant on 2-3 hours visual checks), the resulting trip durations were equally likely to be biased shorter or longer than actual, and, as such errors likely equaled out over time. While the sample sizes were small then, it seem that carrying satellite packs extended the duration of foraging trips throughout the breeding season for birds at Albatross Island. During early chick-rearing, not only were the duration of foraging trips extended but carrying the satellite packs also appeared to result in nest abandonments.

Prior to abandoning, the foraging trip durations of these birds were variable, and ranged up to 6.6 days. As no successful birds had such extended foraging trips early in chick-rearing (Chapter 5), this indicates that carrying satellite packs during this stage was a real disadvantage. Up to and including the 1996/97 studies, all attempts to attach packs to birds post-brood have ended in nest abandonment (Brothers et al. 1998, and Chapter 3). However, successful studies were carried out in 1997/98 when the two smaller satellite packs (0.8-1.1% adult body mass) were deployed on Mewstone birds early in the brooding period. It seems likely that the success of these deployments was due to a combination of the earlier attachment of smaller transmitters.

The effects of carrying devices, and the disturbance caused to breeding albatrosses during the course of satellite tracking work has received little attention. However, nest failures have accompanied a number of satellite tracking studies, including our previous work with Shy albatrosses (Brothers et al. 1998, and Chapter 3), Weimerskirch & Robertson's (1994) study of Light-mantled sooty albatrosses at Macquarie Island, and a number of the Wandering and Royal albatross studies conducted by Nicholls and co-workers (pers. comm.). If such studies are to progress it is critical that field methods be precisely reported (including the breeding period and activity of the instrumented bird when captured, the size and attachment methods of the instruments, the breeding outcomes, and reports of failed/deserting individuals in subsequent years). Dissemination of this sort of information for albatrosses, as has occurred for penguins (Wilson et al. 1997), will aid both appropriate study design, and help minimize impacts upon breeding birds.

8.4.2 *Foraging trip characteristics relative to breeding stage and site*

Shy albatrosses have short duration foraging trips, which average three days or less throughout the breeding season (Chapter 5). However, similar to many seabird species, the duration of foraging trips is adjusted across the breeding season relative to constraints at the nest. The decrease in foraging trip durations from incubation to brood, as well as the similarity found here between the sexes, mirrors findings from a larger study where foraging trip durations were monitored remotely throughout the year (Chapter 5). While sex differences in the foraging zones could only be explored during chick-brood, the aforementioned study indicated that male and female foraging trip durations were similar during all stages of the breeding season. Birds from Albatross Island and Pedra Branca had similar duration foraging trips during incubation, but the maximum foraging range and the total distances covered on these trips, were significantly greater at Albatross Island. Differences in the proximity of the colonies to the shelf edge can perhaps account for this variation. At the closest point, Albatross Island lies approximately 98 km from

the shelf edge, while at Pedra Branca the shelf lies just 37 km away. Birds at Albatross Island therefore nest approximately 2.5 times further from the shelf edge, and at least during incubation this is reflected by a doubling of their maximum foraging range.

8.4.3 *Foraging effort, travelling behaviour and patterns of activity at sea*

Using the average distance moved per hour as an index of foraging effort, Albatross Island birds expended constant effort per foraging day in different years and across different stages of the breeding season. Related to this, the detailed activity data also indicated that the proportion of time spent flying during both the day and the night was similar during incubation and brood (when moon phase was accounted for). There was a clear diurnal pattern, however, with birds moving greater distances per hour during the day than at night.

However, the increase in day-length during summer, which coincides with the chick-brood and early chick-rearing periods (December/January), allows the birds more time for foraging each day. The birds respond to increased day-length by increasing the relative distance covered during the day (from 74% to 82% between incubation and chick-rearing). The decrease in foraging range without an overall corresponding increase in foraging effort, particularly from incubation to chick-brooding indicates that birds either switch prey species between stages, or that a change in resource distribution or abundance results in the prey becoming relatively more available closer to the colonies. It seems that similar to findings for Wandering albatrosses on the Crozet Islands (Salamolard & Weimerskirch 1993), the high energy demands of the brooding period may be at least be partially offset for Shy albatrosses by temporally coinciding with spring/summer blooms in productivity (Harris et al. 1987), combined with lengthy summer days.

The degree of nocturnal activity was influenced by moon phase; birds move further per hour and spend a greater proportion of the night flying during the full moon. Unlike the relationships between moon phase, the proportion of the night spent flying, and the travelling speed at night, there was no relationship between moon phase and the landing frequency per hour. If landings are attempted prey captures, then the fact that their frequency is unrelated to moon phase could indicate that moonlight is used for traveling, but not for foraging, as has been suggested by Weimerskirch et al. (1997d) for Wandering albatrosses. Using leg-mounted activity recorders, stomach temperature sensors and satellite transmitters in tandem, Weimerskirch et al. (1997d) discovered that Wandering albatrosses employ different foraging tactics during the day and the night. During the day much of the prey appeared to be located while the birds were in flight (70% of their

food), whereas during the night prey captures occurred after the birds had spent considerable periods sitting on the sea (30% of the food, Weimerskirch & Wilson 1992). It was concluded that birds actively foraged during the day while at night prey were captured using a sit-and-wait tactic, and foraging was most likely opportunistic (Weimerskirch et al. 1997d).

The nocturnal activity of albatrosses has implications for their incidental capture in longline fisheries. Most seabirds killed on longlines within the AFZ are killed during the day (Gales et al. 1998). As most seabirds are caught attempting to scavenge baits as lines are set (Brothers 1991), one of the most effective ways of reducing seabird by-catch has been to set the lines at night (Brothers et al. in press). However, moon phase influences bird catch rates at night, with more birds caught on a full moon (Vaske 1991, Duckworth 1995, Gales et al. 1998, Brothers et al. in press). While both Shy and Wandering albatrosses, which are primarily diurnally active, increase nighttime activity when the moon is full (this study and Weimerskirch et al. 1997d), the behaviour of primarily nocturnal species such as White-chinned petrels *Procellaria aequinoctialis* which are caught on longlines during the day and night (Murray et al. 1993, Barnes et al. 1997, Gales et al. 1998), is uninfluenced by moon phase (Catard & Weimerskirch 1998). While the vulnerability of certain species is increased during the full moon, the nocturnal habits of other species indicates that they are equally likely be caught at night during any phase of the moon. It is clear then that mitigation techniques such as deploying bird lines and bait casting machines and also consideration of bait thaw state must occur in conjunction with line setting at night in order to reduce seabird by-catch rates.

There was no relationship between wind speed and the proportion of time Shy albatrosses spent flying during the day. This lends support to our earlier findings, where we found that Shy albatrosses did not make extensive use of winds when foraging (Brothers et al. 1998, and Chapter 3). While many albatross species effectively use winds, especially when commuting to and from distant foraging grounds, Wandering albatrosses also do not appear to use winds when foraging in the neritic environment (Weimerskirch et al. 1993). Despite their short foraging ranges, the fact that Shy albatrosses do not make extensive use of winds indicates that they could incur substantial flight costs. Using heart rate recorders, Bevan et al. (1995) estimated that when travelling at high flight speeds on linear routes, the energy expenditure of Black-browed albatrosses was close to basal, but it increased up to four-fold when the birds frequently changed direction and decreased their flight velocity, (presumably when they were actively foraging). Also using heart rate recorders, Weimerskirch (pers. comm.) found that both the heart rate and total energy

expenditure of Wandering albatrosses decreased when they used side winds, a tactic they heavily rely upon during long incubation and chick-rearing trips (Weimerskirch et al. 1993).

The overall travelling speeds of Shy albatrosses are considerably slower than reports for other albatross species (Weimerskirch et al. 1993 & 1994). While this likely relates to the fact that they do not extensively use the wind (and their flight speeds are therefore not strongly wind assisted), as well as the fact that lighter winds are characteristic of their breeding latitude, the slower travelling speeds may also directly relate to their foraging strategy. Shy albatrosses use a searching strategy, and it would seem reasonable to assume that they forage continually while at sea, at least during the day. If this is the case, then, instead of being anomalous the slower flight speeds of this species could likely be adaptive, although, as indicated, flying without making use of the wind is likely to be relatively expensive.

The diurnal pattern of landings on the water was strongest during chick-brood. Birds became increasingly active after sunrise, and the number of landings per hour was high and relatively steady between 7:00-13:00h. There was a second activity peak during late evening between 20:00-22:00h while between 2:00-4:00h and 18:00-20:00h landings were less frequent. The diurnal landing pattern is similar to the species diurnal diving pattern (Hedd et al., unpubl. data) with most dives occurring from early morning to midday with a secondary peak close to dark. The strengths and similarities of these patterns indicate a possible link to the behaviour of their prey. During chick-rearing the diet of Shy albatrosses is dominated by Jack mackerel *Trachurus declivis* and Redbait *Emmelichthys nitidus* (Chapter 6) two species of neritic pelagic fish which occur abundantly in the coastal waters of southern Australia (Williams & Pullen 1993). Mackerel schools form over the shelf during summer and autumn to feed on surface swarms of Australian krill *Nyctiphanes australis.* Schools come close to the surface just after sunrise (returning to depth throughout the day if there is bright sunshine), and they form again near the surface during the last few hours of daylight (Williams & Pullen 1993). There appears then to be some degree of correspondence between the diurnal landing and diving patterns of Shy albatrosses and the schooling pattern of their main prey species.

Comparable data on the manner in which albatrosses partition their time at sea are available for chick-rearing Grey-headed albatrosses from South Georgia and for incubating Wandering albatrosses from the Crozet Islands (Prince & Francis 1984, Weimerskirch et al. 1997d). While incubating, Wandering albatrosses spent 60% of their

total time at sea in-flight, and this is not dissimilar to Shy albatrosses who flew for 50% of the time. When rearing chicks, Grey-headed albatrosses flew for 74% of their total time at-sea, and just 15% of the day and 50% of the night were spent sitting on the sea. The latter values are comparable to brooding birds in this study, although Shy albatrosses averaged less total time in-flight. Considering differences in the species foraging ranges it is perhaps not surprising, as Grey-headed albatrosses commute to distant foraging grounds south of the PFZ when rearing chicks (Prince et al. 1998).

8.4.4 *Foraging zones, foraging strategy and foraging site fidelity*

While the foraging ranges and locations of Shy albatross foraging zones change across the breeding season, the manner in which the birds exploit the marine environment remains constant through time. Within a particular breeding stage, birds concentrate their searching efforts over specific patches of water, but the exact foraging locations within these patches may change from one trip to the next. The fact that birds maintain fidelity to specific patches of water and that these patches differ between individuals indicates that prey is both abundant and widely distributed over Tasmania's continental shelf. However, that the particular foraging location changes from one trip to the next indicates that, while abundant, prey are likely patchily distributed. Presumably though fidelity to the broad area indicates that at this scale, prey are either predictable, or the probability of encountering prey given a certain amount of foraging effort is high (Hunt et al. 1998). It would be interesting in future studies to have some measure of foraging success to link with the albatrosses subsequent degree of area fidelity.

8.4.4.1 *Inter-annual and population-level comparisons*

At the population level, the foraging locations, foraging trip durations and maximum foraging ranges of the birds were highly consistent between years. Such consistency may relate, at least in part, to the relatively consistent oceanographic conditions (SSTs) observed in the vicinity of the colonies during all study years. The only anomalous period was chick-brood 1996/97 at Albatross Island when there was a spatial shift in the foraging zone between years. Whereas chick-brooding birds generally foraged north of Albatross Island either east or west of King Island, there was a southerly shift during 1996/97, and birds fed west-southwest between the colony and the edge of the continental shelf. In general, the high predictability in foraging locations indicates that the distribution and/or abundance of prey was relatively consistent between years. The shift during brood in 1996/97, however, did indicate some inter-annual variability, either with the locations of the prey themselves, or perhaps more widely to variations in the

oceanographic conditions. This shift, however, was not reflected in any obvious way by changes in SSTs.

Different water masses influence the foraging grounds of the three populations, and because of this, the magnitude of any inter-annual differences in foraging locations or prey availability might be expected to vary between the sites. Little is known of the oceanography off western Tasmania, however, the east coast is comparatively well studied. There are strong inter-annual variations in regional oceanography off Tasmania's east coast, and these relate to the relative degree of influence of the subtropical East Australian current. This current is warm and nutrient-poor and in years when it strongly influences waters over the shelf, there is a decrease in both the biomass and diversity of zooplankton (Young et al. 1993 & 1996). A decrease in krill *Nyctiphanes australis* biomass results in a decrease in the surface schooling patterns of Jack mackerel that form to feed on them (Young & Davis 1992, Williams & Pullen 1993). Given the importance of Jack mackerel to the diet (Chapter 6), years when its abundance was decreased might be expected to be poor years for albatrosses breeding at Pedra Branca. Oceanographic features of the foraging zones of Albatross Island and Mewstone birds would be most effected by the Zeehan and Leewin currents, however, less is known of the characteristics of these currents in Tasmanian waters, or how inter-annual variations in their influence may affect biological productivity.

Despite the relative proximity of the colonies, albatrosses from the three populations use mutually exclusive foraging zones during the breeding season. The exclusive nature of the populations and their consistent foraging locations, indicate that the populations have traditional foraging grounds.

8.4.4.2 *Comparison with other species*

Few studies have examined the consistency in foraging zone locations of either individual seabirds or populations at different temporal scales. However, comparing the degree of foraging site fidelity observed here with the data that do exist is difficult because of problems with scale, coupled with the fact that many previous studies have not been quantitative. Nevertheless, when brooding chicks, Wandering albatrosses from the Crozet Islands use short commuting flights, to repeatedly exploit specific areas along continental shelf breaks (Weimerskirch et al. 1993, Weimerskirch 1998b). However, it was unclear what degree of consistency was required before a bird was assumed to show area fidelity.

Black-browed albatrosses at Kerguelen Island are also reported to show area fidelity (Weimerskirch et al. 1997c, Weimerskirch 1998b). These birds also forage solely in neritic waters, repeatedly using areas along the eastern Kerguelen shelf break, or a small shelf north of Heard Island on successive trips to sea. Despite both species foraging in the neritic zone, the foraging strategies of Shy and Black-browed albatrosses at Kerguelen Island are actually quite different. Black-browed albatrosses commute quickly to the shelf edge where they spend the majority of their time before returning to the colony. Like a number of seabird species (Bost et al. 1997, Hull et al. 1997), Black-browed albatrosses at that site are thought to be exploiting resources located within the Antarctic Polar Frontal Zone (PFZ) a northeast meandering of which runs parallel with the shelf break at Kerguelen Island (Weimerskirch et al. 1997c). Frontal zones are generally areas of enhanced productivity (Park et al. 1993), and within Antarctic/sub-Antarctic waters, myctophid fish which are major prey species of albatrosses and penguins, occur closer to the surface and in higher concentrations within the PFZ (Gon & Heemstra 1990). Presumably the proximity of the PFZ to the colony provides abundant resources for the Black-browed albatrosses at Kerguelen Island and this could perhaps account for the consistency in their foraging locations between years (Weimerskirch et al. 1997c, Weimerskirch 1998b).

Other studies have indicated area fidelity during the breeding season; Black-legged kittiwakes *Rissa tridactyla*, where birds return to the same general areas to forage on the majority of their trips to sea (Irons 1998), a finding similar to Becker et al. (1993) for Common terns *Sterna hirundo*. However, in a three year study of Shags *Phalacrocorax aristotelis* Wanless et al. (1991) found significant inter-annual variation in the location of the foraging zones, and presumed these differences were related to changes in the distribution of sandeels *Ammodytes* spp., a predominant dietary taxa during that time. In marine environments where prey can be located with some degree of spatial and temporal predictability, it seems that individual seabirds cue in to and repeatedly use areas where they have successfully foraged, at least in the short term. Presumably due to a combination of environmental factors and dynamic constraints at the nest, for Shy albatrosses this system seems to operate within the time frame of a single breeding stage.

8.4.5 *Differential at-sea distribution of the three populations: implications for interactions with longline fisheries*

The foraging zones of the three Shy albatross populations in Tasmania are mutually exclusive during the breeding season (Figure 8.16). The populations south of Tasmania (Pedra Branca and Mewstone) are restricted to southeast and southwestern waters,

respectively, while birds from Albatross Island forage mainly over the continental shelf between northwest Tasmania and Victoria. Limited information from Albatross Island and Pedra Branca indicates that outside the breeding season birds are sedentary, and they remain in southeast Australian waters year round (Brothers et al. 1997, 1998, and Chapter 3). We have no information on the wintering grounds of Mewstone birds, and this is a concern given that Mewstone holds almost 60% of this species breeding pairs. Information from band returns, colour-marking, and satellite tracking studies indicates that juvenile birds are more widely distributed than adults, and their migration routes are population specific (Brothers et al. 1997, Hedd et al. unpubl. data). While fledglings from Albatross Island are restricted to Australian waters, those from Mewstone have been found both off New Zealand and South Africa (Brothers et al. 1997). The wider distribution of fledglings exposes them to more fisheries than those which threaten the adults, and by-catch in both legal and illegal fisheries operating in the Southern Ocean is a concern.

From the 1950's to late in 1997, the Japanese fished for Southern bluefin tuna in Tasmanian waters, mainly concentrating their efforts along the south, west and east coasts (Caton et al. 1995). Seabird by-catch rates in this fishery were variable through time, with more birds overall caught in summer than winter, and also space, with higher catch rates on Tasmania's west than east coasts (Gales et al. 1998). Given the consistency in albatrosses foraging locations between years, we can speculate that from its inception, the Japanese fishery would have had serious impacts upon the albatrosses breeding at Pedra Branca and Mewstone, but less probable impact upon the population at Albatross Island.

The Trilateral Agreement between Japan, Australia and New Zealand for annual quota limits of Southern bluefin tuna failed to be ratified for 1998. This resulted in the Japanese being denied access to fish for tuna within the AFZ, and by default, the fishery moved outside the foraging zones the resident albatross populations. However, concomitant increases in the Australian domestic longline fishery have largely replaced the Japanese effort, and are cause for continued concern. The domestic fishery also has a significant seabird by-catch problem (Brothers & Foster in press), and as it operates using smaller, mainly non-purpose built vessels, the fishing occurs further inshore. This feature heightens the potential for overlap with the resident albatrosses. Levels of overlap between the albatrosses and this fishery between 1995/96 and 1997/98 were similar to levels reported for the Japanese portion of the fishery. Birds from Pedra Branca, then, are at risk of being caught in fisheries operating along the south and east coasts of Tasmania, while birds from Mewstone would be vulnerable to fisheries operating along the south

and west coasts. Given the distribution of the fisheries, breeding birds from Albatross Island would be vulnerable only at the southern limit of their foraging range, along Tasmania's mid-west coast.

Temporary area and/or seasonal fishery closures have been proposed as a method to reduce the overlap and hence the by-catch of seabirds in areas where seabird/fishery interactions are known to be high (Alexander et al. 1997, Environment Australia, 1998). For example, longline fishing could be prohibited around breeding colonies during the chick-brooding phase when albatross foraging ranges are reduced, and overlap between the birds and fisheries is high at or near continental shelf edges (Weimerskirch et al. 1993, Croxall & Prince 1996b, Brothers et al. 1998, and Chapter 3). The foraging zones of Shy albatrosses are consistent from one year to the next, making area or seasonal closures an option, at least in principal, for reducing catch rates of this species. However, we do not advocate this approach, as exclusion zones will simply result in fisheries moving elsewhere, and in doing so, they will likely just catch other species. In other words, this solution would not address the reasons why seabirds become caught on longlines, it would rather simply shift the problem from one area or species to another.

8.4.6 *Influence of other fisheries on the at-sea distribution of Shy albatrosses*

Similar to many other albatross and seabird species, Shy albatrosses are enthusiastic scavengers behind fishing vessels. There is extensive correspondence between the foraging zones of breeding Shy albatrosses and vessels fishing in the South-east trawl, Southern Rock Lobster and Tasmanian Finfish fisheries. However, as we do not have comparable information on the distribution of birds prior to commencement of these fisheries nor do we know if any of the instrumented birds attended fishing vessels, it is not possible to quantify the extent of fisheries influence on the distributions we report. If, however, we accept that Shy albatrosses behave similarly to other vessel-attracted species, for which such information exists, we may expect that their overall distribution has not been altered (Freeman 1997, Prince et al. 1998, Weimerskirch 1998b). Prince et al. (1998) report that despite extensive correspondence between the distribution of Wandering albatrosses from South Georgia and the distribution of longline and trawling vessels, that many of the overlapping areas were actually favored by the albatrosses prior to fisheries development. Similarly, correspondence of the foraging zones of Black-browed and Wandering albatrosses from Kerguelen Island in years with and without fishing activity indicates that although birds attend fishing vessels when they occur within their foraging areas, their overall distributions were not altered (Weimerskirch 1998b). It seems likely then that certain areas are attractive to albatrosses and fisheries alike because

of their high productivity levels and the associated aggregations of prey they support (Prince et al. 1998). Taken together, these studies, along with that of the Westland petrel *Procellaria westlandica* (Freeman 1997) suggest that, at least for some species, while boats may act as artificial aggregators of birds, they do not appear to affect their overall distributions.

8.4.7 *Conservation implications and future directions*

The mutually exclusive foraging zones of the three Shy albatross populations in Tasmania result in differential vulnerability to longline fisheries. Unfortunately the status of the Tasmanian populations is known only at Albatross Island, where the population is recovering from dramatic declines exacted by feather hunters and egg collectors at the turn of the Century. The current population (5,000 pairs) is thought to comprise just 25% of the original population size (estimated by N. Brothers), but numbers have increased from just 300 nests in 1909 (Johnstone et al. 1975, N. Brothers, unpubl. data). Unfortunately trends in the population size at Pedra Branca and Mewstone (which holds almost 60% of the breeding pairs of the species) are unknown (Gales 1998). As it is likely albatrosses from Pedra Branca and Mewstone that are being killed in local longline fisheries, determining the status of these populations is a priority.

This study clearly indicates the importance of considering the impacts of fishing upon albatrosses at the population, and not the species, level, and this has implications for the development of long-term monitoring programs. Despite the proximity of the three Shy albatross populations, because of their at-sea distribution they are under considerably different threats from fishing activities. A similar situation has also been reported for Black-browed albatrosses at Kerguelen Island, where the at-sea distribution of two colonies differentially exposes them to longline fishing (Weimerskirch et al. 1988, Weimerskirch 1998b). While the colony on southern Kerguelen Island shows no overlap with longline fisheries, the colony to the northwest overlaps with fisheries throughout the breeding season (Weimerskirch 1998b).

Along with by-catch in longline fisheries, Shy albatrosses are also killed in trawl fisheries within the Tasmanian region (N. Brothers, pers. comm.). In New Zealand, large numbers of Shy albatrosses were killed through collision with netsonde monitor cables, thin cables running from the stern of the trawler to the trawl net (Bartle 1991). It was estimated that 2,300 Shy albatrosses died in this manner in 1990, and by 1991 the use of netsonde monitor cables were banned in New Zealand's 200 mile Exclusive Economic Zone (Bartle 1991). While death rates in Australia's southeast trawl fishery have not been quantified

the extent of trawling occurring within the albatross foraging zones indicates that the numbers could be substantial.

Aside from direct mortality associated with longline and trawl fisheries, albatrosses also potentially suffer indirectly from commercial fisheries that target their main prey species. Throughout the period of chick care, the diet of Shy albatrosses is dominated by fish (approximately 80%) and squid (less than 20% by fresh mass). Jack mackerel and Redbait are the major fish components, while Gould's squid *Nototodarus gouldi* is the most frequently consumed cephalopod species (Chapter 6). Jack mackerel and Gould's squid are both the targets of commercial fisheries in Tasmania. A large volume purse-seine fishery targeting surface or near surface schools of Jack mackerel commenced in 1985, and it has taken between 10,000 and 42,000 tonnes per year since that time (McLoughlin et al. 1995). The fishery runs from October to May, and as much as 95% of the annual catch comes from eastern Tasmanian State waters (McLoughlin et al. 1995). The fish is used to produce fishmeal and petfood, and ironically, it is used as bait in both the longline and local Rock lobster fisheries (Kailola et al. 1993). There is a small jig fishery for Gould's squid in western Bass Strait, which lies within the foraging zone of the Albatross Island population. The majority of the squid are taken in Western Victoria, and catches peak during April and May. While the annual catch has been just a couple of hundred tonnes since the mid 1980's, a catch of 1,800 tonnes in 1995 has renewed interest in the fishery (McLoughlin et al. 1997). According to fisheries management authorities the stock is underexploited, and there have been calls for further fishery development (McLoughlin et al. 1997). Clearly, commercial overexploitation of either Jack Mackerel or Gould's squid would have detrimental impacts upon the albatross populations. The food requirements of these predators, along with those of Australasian gannets *Sula serrator*, Australian and New Zealand fur seals *Arctocephalus pusillus doriferus* and *A. forsteri*, which also rely heavily upon these prey species (Brothers et al. 1993, Gales et al. 1993, Gales & Pemberton 1994, Lake 1997), must be considered in any responsible management of these resources.

For many albatross populations declines are the result of critically low recruitment levels. Juvenile albatrosses are highly migratory, and are exposed to a wider variety of fishing activities (longlining, trawling etc) than those which impact upon adults and adult survivorship, and in this respect Shy albatrosses are no exception (Brothers et al 1997, 1998, Chapter 3 & this study). The life history characteristics of albatrosses (delayed maturity, low reproductive output) make them particularly vulnerable to any anthropogenic influences which affect their survival. Longline or other sources of

mortality would exacerbate problems of naturally low breeding success (as is the case at Mewstone, N. Brothers pers. comm.), even further lowering levels of recruitment into the breeding population. Given the dearth of information on the distribution of juvenile and adult Shy albatrosses outside the breeding period, future studies must focus both on identifying the foraging zones of these portions of populations, as well as encouraging widespread adoption of appropriate mitigation measures, if fisheries and albatrosses are to co-exist in the long-term.

Chapter 9

GENERAL DISCUSSION

9.1 THE PROBLEM

The stimulus for this work originated from the realization in the early 1990's (Brothers 1991) that large numbers of seabirds, mainly albatrosses and petrels, were taken as by-catch in Japanese tuna *Thunnus spp.* longline fisheries south of 30°. Combining data on the incidental mortality of seabirds with information from long-term population studies, it was gradually realized that longline fisheries were responsible for observed declines in albatross populations worldwide (Croxall & Prince 1990, Brothers 1991, Weimerskirch et al. 1992, Prince et al. 1994). Subsequently a global review of the status of albatross populations indicated that over half of those studied were either currently, or in the past they had been, in decline (Gales 1993). The extent of mortality exacted by longline fisheries, and the implications of this for trends in population size, depend largely upon the nature of interactions between the birds and fisheries operating within their foraging zones.

Until the end of 1997 there was both a Japanese and an Australian domestic longline fishery for Southern Bluefin tuna *Thunnus maccoyii* operating within the Australian Fishing Zone (AFZ). Seabird by-catch in the Japanese portion of the fishery has averaged at least 0.15 birds/1000 hooks over the past decade, and this translates into mortalities of at least 1,000-3,500 birds per year (Gales et al. 1998). In the past 10 years a minimum of 5,000 Shy albatrosses (*Thalassarche cauta* plus *T. steadi*, in unknown proportions) have been killed on Japanese vessels in the AFZ (Gales et al. 1998). While this fishery has since ceased in the area, there is continued concern for the conservation of seabirds as the Japanese effort has been largely replaced by the Australian domestic fishery. Shy albatrosses are also the most frequently caught species in this fishery (Tasmanian Parks & Wildlife Service, unpubl. data), however estimates of the total numbers killed are unavailable.

9.2 THE SPECIES

Shy albatrosses *Thalassarche cauta* are endemic to Australia, and they breed in three colonies off the coast of Tasmania; Albatross Island to the north, with 5,000 breeding

pairs per year, and Pedra Branca and Mewstone off the south coast, with 250 and 7,000 pairs per year, respectively. The total breeding population size is therefore ≈12,250 pairs (N. Brothers, unpubl. data). On the basis of their restricted breeding distribution the species is listed as *Vulnerable* both globally and under Australian legislation (IUCN, Croxall & Gales 1998).

The status of the populations is known only at Albatross Island, where numbers are slowly recovering from dramatic declines exacted by feather hunters and egg collectors at the turn of the Century. The current population at that site is thought to comprise just 25% of the original population size (estimated by N. Brothers), but numbers have increased from just 300 nests in 1909 (Johnstone et al. 1975, N. Brothers, unpubl. data). Unfortunately trends in the population size at Pedra Branca and Mewstone, which collectively hold 60% of the breeding pairs, remain unknown (Gales 1998). Furthermore it is these latter populations which are likely to be most seriously impacted by longline fisheries (Brothers et al. 1997 & 1998).

Despite the prevalence of Shy albatrosses in the by-catch of longline fisheries, Croxall (1998) notes that it is one of the least known of the albatross species. The broad aim of this project, then, was to redress this inadequacy by examining integrated aspects of the breeding and foraging ecology of this species and to assess the extent of its overlap with longline fisheries operating within the AFZ.

9.3 THE PROJECT

The aims of the project were:

1) to quantify aspects of the species foraging ecology by:

   - identifying the foraging locations using satellite telemetry; conducting both inter- and intra-annual comparisons of foraging zone use;
   - investigating both the diving capabilities of the birds and their behaviour at sea using archival data loggers;
   - quantifying the diet composition during the chick-rearing period, and documenting any inter-annual variation;

2) to examine the parental investment and breeding strategies of adults by:

   - monitoring annual patterns of adult attendance at two of the breeding sites;
   - documenting the chick provisioning and growth strategies throughout the rearing period

3) to determine the level of interaction of the birds with fishing operations by:

- determining for each population the degree of overlap with Japanese and Australian domestic longline fisheries within the AFZ;
- estimating the proportion of the diet originating from fisheries discards.

Whilst fieldwork was conducted at the three breeding sites, and across three breeding seasons (1995/96 to 1997/98), work was focused at Albatross Island.

While detailed discussions of the findings from each aspect of the study were considered separately in Chapters 2 through 7, this general discussion will synthesize the information and present an integrated account of the ecology of the Shy albatrosses inhabiting the coastal waters off southeast Australia.

9.4 ALBATROSSES IN GENERAL

The recent revision of the taxonomy of the Diomedeidae (Nunn et al. 1996, Robertson & Nunn 1998) has identified 24 species of albatrosses, and the breeding distribution of these species ranges from the tropics to the sub-Antarctic, and spans both hemispheres. While much of the detailed early work on albatross breeding biology originated from the tropical species (Rice & Kenyon 1962, Fisher 1975 & 1976), most of our current knowledge of the habits, foraging ecology, and life-history characteristics of albatrosses derives from populations breeding within the sub-Antarctic. Most of this information has come from South Georgia (54° S) in the South Atlantic and from Kerguelen and Crozet Islands (46-50° S) in the Southern Indian Ocean. However, general ecosystem processes, including the physical and biological oceanographic features of the foraging zones, are central to understanding key ecological differences between species; including clear differences between the temperate breeding Shy albatrosses and the species breeding in the sub-Antarctic. While temperate species are often considered together with the polar species, it is clear from this study that the foraging and breeding strategies can be remarkably different.

9.5 SHY ALBATROSSES

Shy albatrosses breeding in Tasmania appear to show more flexibility and more variability in their foraging and breeding parameters than other, less temperate species. Or, to put this differently, the species seems to be operating in an environment that allows them a "larger margin for error". Differences in aspects of their breeding biology and foraging ecology, then, perhaps reflect the less demanding features of their environment.

9.5.1 *Foraging trip durations and foraging zones between years*

While most albatross species spend at least a portion of their breeding period foraging in pelagic waters (Table 9.1), Shy albatrosses forage exclusively in the neritic zone. Shy albatrosses forage over the southeast Australian continental shelf within 200-300 km of their colonies (Brothers et al. 1997, 1998, Chapters 3 & 8). Consistent with their foraging locations, Shy albatrosses have short duration foraging trips (averaging 1-3 days) throughout the breeding season (Chapter 5). However, as has been demonstrated for other species, there is also a predictable spatial shift in foraging zone use at Albatross Island, as the breeding season progresses; with birds feeding closer to the colonies when chicks hatch. This is a common feature of albatross breeding strategies, and the duration of foraging trips for all species shorten to between one and three days during the brooding period (Table 9.1, Chapter 5). The contraction of both the foraging range and foraging trip duration is necessary to ensure that young chicks receive regular feeds soon after hatching.

While foraging over the shelf, Shy albatrosses use a searching strategy to locate their prey (Chapter 8). Individual birds exhibit a high degree of foraging site fidelity, using the same broad areas of the continental shelf from one trip to the next. Different individuals use different foraging areas indicating that while food is abundant, its distribution is likely patchy. The abundance of resources has allowed a certain degree of flexibility in the breeding strategy, at least during the incubation period. There is substantial individual variability in the mean duration of foraging trips and shifts at the nest during this stage of the breeding season, indicating that a wide range of attendance and foraging patterns can carry pairs through this stage. Flexibility during incubation is also obvious from the birds propensity to refuse shift changes at the nest. That is, when a mate arrives in the colony there is not necessarily a swapping of duties. Incubating birds refuse to go to sea on approximately 20% of arrivals.

Despite substantial individual variability, at Albatross Island the duration of foraging trips and shifts at the nest was highly consistent between years. Duties at the nest were shared equally, with males and females having similar duration foraging trips and shifts on the nest throughout the breeding season. Equal sharing of duties at the nest during the incubation period is consistent with findings for Black-browed *Thalassarche melanophris* and Grey-headed albatrosses *T. chrysostoma,* but contrasts with the situation for Wandering *Diomedea exulans* and Light-mantled Sooty albatrosses *Phoebetria palpebrata* where males contribute significantly more (Croxall & Ricketts 1983, Weimerskirch et al. 1986). There is much less information regarding the sharing of

Table 9.1: Summary of the key breeding and foraging ecology parameters for some of the better-studied albatross species. Aspects of Shy albatrosses ecology which have been elucidated and/or quantified by this study have been shaded grey.

Parameter	Wandering[1]	Black-browed[2]	Grey-headed[3]	Sooty[4]	Light-mantled[5]	Yellow-nosed[6]	Shy[7]	Southern Buller's[8]	Laysan[9]	Black-footed[10]	Waved[11]
Breeding frequency	Biennial	Annual	Biennial	Biennial	Biennial	Annual	Annual	Annual	Annual	Annual	Annual
Breeding locality	sub-Antarctic	sub-Antarctic	sub-Antarctic	sub-Antarctic	sub-Antarctic	Temperate sub-Antarctic	Temperate	Temperate	Tropical	Tropical	Tropical
Foraging trip duration	Long	Short/Long	Long	Long	Long	Long	**Short**	Long	Long	Long	Long
Incubation	Short	Short	Short	Short	Short	-	**Short**	Short	Short	Short	Short
Brooding	Short/Long	Short	Short	Long	-	Short/Long	**Short**	-	-	-	-
Chick-rearing											
Winter attendance	no	no	no	no	no	no	**yes**	no	no	no	no
Foraging locality											
Incubation	Pelagic	Neritic	Pelagic	Pelagic	Pelagic	-	**Neritic**	Pelagic	-	Pelagic	Pelagic
Brooding	Neritic	Neritic	Neritic	Pelagic	Pelagic	-	**Neritic**	-	-	-	-
Chick-rearing	Neritic/Pelagic	Neritic	Neritic/Pelagic	Pelagic	-	Pelagic	**Neritic**	-	-	Pelagic	-
Diet (% fresh mass)								FOO(%)			FOO(%)
Fish	15 - 42%	26 - 82%	< 1 - 61%	6 - 33%	11 - 46%	58%	**84%**	48%	9%	50%	41%
Cephalopods	40 - 77%	1 - 74%	34 - 89%	41 - 42%	34 - 56%	38%	**11%**	30%	65%	32%	53%
Crustacean	< 1%	< 1 - 42%	3 - 32%	1 - 3%	16 - 40%	4%	**2%**	44%$	9%	5%	10 - 46%
Other	5 - 19%	0 - 8%	0 - 5%	25 - 51%	4 - 17%	0%	**3%**	19 - 26%	17%	13%	?
Chick-provisioning											
Fledging period	278	116 - 130	141	145 - 178	157	115	**127**	167	165	140	167
Feeding frequency (days)	1.8 - 2.8	1.22 - 1.9	1.26 - 2.28	2.71	2.90	-	**0.92**	-	2.46	2.87	-

[1]Croxall & Ricketts 1983, Prince & Morgan 1987, Cooper et al. 1992, Weimerskirch et al. 1993, Ridoux 1994, Weimerskirch et al. 1997b; [2]Tickell & Pinder 1975, Prince 1980, Croxall et al. 1988, Thompson 1992, Rodhouse & Prince 1993, Reid et al. 1996, Weimerskirch et al. 1997c, Waugh & Weimerskirch 1998, Prince et al. submitted; [3]Tickell & Pinder 1975, Prince, 1980, Prince et al. 1981, Weimerskirch et al. 1986, Croxall et al. 1988, Hunter & Klages 1989, Ridoux 1994, Reid et al. 1996, Prince et al. 1998, Prince et al. submitted, [4]Berruti 1979, Weimerskirch et al. 1986, Ridoux 1994, Cooper & Klages 1995, Weimerskirch 1998b; [5]Berruti 1979, Thomas et al. 1983, Weimerskirch et al. 1986, Ridoux 1994, Cooper & Klages 1995; [6]Jouventin et al. 1983, Weimerskirch et al. 1986, Weimerskirch 1998b; [7]N. Brothers unpubl. data, Brothers et al. 1998, this study; [8]West & Imber 1986, Sagar & Weimerskirch 1996, Sagar & Warham 1998; [9&10]Rice & Kenyon 1962, Harrison et al. 1983; [11]Harris 1973, Anderson et al. 1998

parental duties during other breeding stages. At the population level the foraging zones were also highly consistent between years, with birds foraging in much the same location from one year to the next. There was also no indication of sex segregation at sea, with males and females utilizing much the same foraging areas. This contrasts with the situation for Wandering albatrosses where the sexes segregated at sea during incubation and also during the chick-rearing period (Prince et al. 1992, Weimerskirch et al. 1993, 1997b).

Despite their proximity, foraging zones of the three Tasmanian Shy albatross populations are mutually exclusive during the breeding season. Birds from Albatross Island forage in waters off northwest Tasmania, while birds from Pedra Branca and Mewstone forage off the southeast and southwest coasts, respectively. A similar situation exists at Kerguelen Island where two colonies of Black-browed albatrosses use separate foraging zones at sea (Weimerskirch et al. 1986, Weimerskirch 1998b). Mutually exclusive foraging zones were certainly not expected for Pedra Branca and Mewstone as the colonies lie just 40 km apart. Spatial separation of the foraging zones is not only fascinating from an ecological perspective, but it also has far reaching conservation implications. Specifically, both the distribution of effort in the longline fisheries and differences between areas in seabird guilds result in different seabird by-catch rates in the areas around Tasmania. As most fishing occurs off the south, east and west coasts, birds from Albatross Island remain relatively remote from the fishing operations (Brothers et al. 1998, Chapters 3 & 8). Seabird by-catch is high, yet characteristically different, off the east and west coasts of Tasmania (Gales et al. 1998), and as a result, birds from Pedra Branca and Mewstone would likely suffer different levels of incidental mortality. However, equally importantly, the different exposure of these three populations to longline fishing confirms the necessity of monitoring studies to focus at the population, and not the species level.

9.5.2 *Over-winter attendance at the colony*

The highly migratory nature of adult albatrosses outside the breeding season (Nicholls et al. 1992, 1995, 1997, 1998, Prince et al. 1998) is interpreted to indicate that there is decreasing prey availability in the vicinity of the colonies. While adults from all other known albatross populations traverse the oceans searching for food in the non-breeding period (Table 9.1), adult Shy albatrosses from Albatross Island remain close to the colonies year-round. Adults typically spend just eight weeks at sea after fledging their chicks, and during this time they also forage in the waters off southeast Australia. This species, then, is relatively sedentary once reaching breeding age (Brothers et al. 1997 &

1998, Chapter 3). After they return, adults spend much of the Austral winter attending the colony, interspersing periods at the nest with generally short foraging trips to sea (less than two weeks duration). The proportion of time birds spend in attendance at the colony increases as the next breeding season approaches. While there was some individual variation in arrival times, all birds arrived at the colony well in advance of the next breeding season, with even the latest arrivals returning 10 weeks prior to egg-laying.

There was a sex difference in the pattern of attendance at the colony during the non-breeding period. Males arrived back to the colony, on average, 10 days earlier than their mates, and they subsequently spent more time attending the site. The earlier return of males to the colony is consistent with patterns for Wandering, Black-browed and Grey-headed albatrosses where males also arrive a week to ten days prior to their mates (Tickell 1968, Tickell & Pinder 1975). While the same tendency was noted for Laysan albatrosses, no quantitative data were given (Rice & Kenyon 1962). Shy albatrosses display a high degree of nest site fidelity and while both sexes will defend the territory against intruders, males in particular are quite aggressive. While males spend much of their time defending and maintaining the nest site over-winter, the amount of time pairs spend together indicates that this is also an important time for reinforcing the pair bond.

The proximity of Shy albatrosses to the breeding colonies over-winter indicates that food is available within the vicinity of the colony year-round. While Jack mackerel is the most important prey species of Shy albatrosses during the chick-rearing period (Chapter 6), its seasonal availability in surface waters indicates that during winter at least, the birds must exploit alternative prey species. It seems likely that there is a seasonal diet shift from mainly fish during the chick-rearing period to mainly squid in winter. However, irrespective of the composition of the diet, the availability of food year round is confirmed by the influx of migrating albatrosses to the waters surrounding Tasmania in winter (Barton 1979, Reid et al. in press, T. Reid, unpubl. data).

Shy albatrosses are only sedentary once reaching breeding age. Banding and colour marking studies revealed that juveniles are highly migratory, and their movements are population specific. Juveniles from Albatross Island appear to remain in Australian waters, while those from Mewstone traverse the Southern Ocean, with resighting records from New Zealand to South Africa (Brothers et al. 1997). Limited support for differential population movements was obtained from a recent pilot study of the foraging movements of juveniles during their first three months at sea. Juveniles from both Albatross Island and Pedra Branca moved to the shelf area near Kangaroo Island (off South Australia) where they remained over the next three months. The chick from Mewstone exhibited

somewhat of a different pattern, moving first to the waters off South Australia but then subsequently to Western Australia. The satellite transmitter on the chick from Mewstone ceased functioning when the bird was approximately 500 km southwest of the Western Australia coastline (Hedd, Gales & Brothers, unpubl. data).

9.5.3 *At-sea activity patterns, diet and foraging techniques*

Despite the deep-water habits of many squid species, the importance of this prey class to the diet of many albatrosses (Table 9.1) leaves some uncertainties regarding the manner in which prey are captured (Croxall & Prince 1994, Cherel & Klages 1998). That is, for some species it is unclear whether the prey are mostly predated and taken live or if they are scavenged at the surface after death. The situation for Shy albatrosses seems clear.

Much (> 80%) of the distance covered per day by Shy albatrosses is covered during daylight (Chapter 8). Diving forms a significant part of the foraging repertoire of Shy albatrosses (Hedd et al. 1997, Chapter 4), as it does for a number of other small albatross species (Prince et al. 1994, Huin & Prince 1997), with birds capable of diving to 8 m depth. While olfactory cues may be used to locate prey (Nevitt et al. 1997, Nevitt & Veit 1998), the strictly diurnal diving patterns of Shy albatrosses indicates that the birds rely heavily on sight to locate their prey (Hedd et al. 1997, Chapter 4). During the period of chick care in all years the diet was dominated by three species; Jack mackerel *Trachurus declivis*, Redbait *Emmelichthys nitidus* and Gould's squid *Nototodarus gouldi*. These species school in surface waters during the day where they are naturally available to the albatrosses. Combining information on the behaviour of the albatrosses at sea and the behaviour of their main prey, it seems clear that Shy albatrosses are largely predatory, and they can take most, if not all, of their prey from surface waters during the day.

Examination of the diet revealed that Shy albatrosses also exploit the discards or by-catch from trawling operations, as some of the fish consumed were benthic inhabitants, and species known to figure substantially in the by-catch of trawlers operating off western Tasmania (Last et al. 1983). Scavenged material, however, contributed minimally to the diet. By number, scavenged fish contributed between 5 and 18% to the diet, however, there was little evidence to suggest that any more than 3% (by number) of the squid were obtained in this manner. Despite the extent of trawling operations within the foraging zone of the Albatross Island population (Chapter 8), it does not appear that discards are heavily relied upon to fulfill the energy requirements of the birds, at least during the chick-rearing period.

9.5.4 *Provisioning rates to chicks*

The proximity of the foraging grounds to the breeding colony, coupled with the relative abundance of prey result in Shy albatrosses having one of the highest feeding frequencies and shortest fledging periods of the albatrosses thus far studied (Table 9.1). Shy albatross chicks are fed, on average, every 0.92 days throughout the rearing period, a frequency almost three times higher than for Sooty *Phoebetria fusca*, Light-mantled Sooty *P. palpebrata*, Black-footed *Phoebastria nigripes* and Wandering albatrosses, from some sites (Table 9.1 and references cited therein). Feeding frequencies were similar to those of Black-browed and Grey-headed albatrosses at South Georgia, which are fed every 1.22 and 1.26 days, respectively (Prince et al. submitted). Shy albatrosses provisioned their chicks in the order of 400 g/day from the end of the brooding period until fledging. An estimated 45 kg of food was required to raise a chick.

While there were no consistent adult sex differences in provisioning performance, there were differences in overall provisioning rates to male and female chicks (Chapter 7). Female chicks received an estimated 37.6 ± 0.21 kg (n=3) between hatching and fledging, while male chicks received a total of 47.7 ± 0.14 kg (n=3). Chicks are sexually dimorphic at fledging (Hedd et al. 1998, Chapter 2), and while the sexes are provisioned at the same relative rate ($g/kg^{0.75}$/day), male chicks remain on the nest for 10 days longer and receive almost 10 kg more total food than females. Weimerskirch (pers. comm.) has also found sex differences in the food requirements of male and female Wandering albatross chicks. It seems clear that chick sex is another variable that must be factored into studies examining the patterns and regulation of food delivered to chicks.

Locally accessible food resources enable some Shy albatrosses to increase provisioning rates when their chicks are hungry. There were indications in this study, however, that this capacity related to the 'quality' of the adult, as some parents were able to increase provisioning rates to their chicks while others were not. The superior ability of some parents was exemplified by increased chick feeding frequencies when adults raised their chick alone. Single parents were observed to successfully fledge chicks after feeding them alone for periods ranging between 6 and 12 weeks. This corresponded with single parent feeding from the time that chicks were aged as young as four weeks. Single parent feeding has also been noted for Black-browed albatrosses at Kerguelen Island (Weimerskirch et al. 1997c), however, the fate of those chicks was unfortunately not noted.

When considered within the ecological framework developed for sub-Antarctic

Procellariiformes by Weimerskirch and colleagues (1995, 1997b, 1997c), the possibility of Shy albatrosses being able to increase the rate of food delivery to chicks would not have been expected. Weimerskirch et al. (1995, 1997b, 1997c) reasoned that because neritic species perform only short duration foraging trips, they were probably already delivering food at a maximum rate and would therefore have little capacity to further increase their provisioning rates. It was suggested that the evolution of the two-fold foraging strategy described for pelagic species (Chaurand & Weimerskirch 1994b, Weimerskirch et al. 1994, 1997b) would instead provide adults more flexibility in responding to chick demands. Pelagic species undertake both short and long duration foraging trips when rearing chicks, and species such as Thin-billed prions *Pachyptila belcheri* have been shown to be able to increase their provisioning rates by increasing the proportion of time spent in short foraging trips (Weimerskirch et al. 1995). Whereas Black-browed albatrosses were unable to increase provisioning rates when their chicks were hungry, this capacity was evident for Shy albatrosses breeding at Albatross Island. Foraging exclusively within the neritic environment did not cap the provisioning capacity of this species, rather it seems that exploiting abundant local resources actually enabled it.

9.5.5 *Periods of stress*

Despite inhabiting a locally rich environment, there was some indication that two periods (brood and mid to late chick-rearing) were particularly stressful. The consistent duration of foraging trips between individuals, breeding sites and years, coupled with a decline in body mass indicates that the brooding period is relatively energetically stressful for this species. The brooding period has been shown to be stressful for a number of other albatross species, as similar declines in body mass have been noted for Black-browed, Grey-headed and Wandering albatrosses (Croxall 1990, Salamolard & Weimerskirch unpubl. data, cited in Salamolard & Weimerskirch 1993). As most nest desertions occurred between mid and late chick-rearing this is also clearly an energetically taxing period for Shy albatrosses.

Given the short duration of foraging trips and the neritic foraging habits of Shy albatrosses, long-term fasting is not a requirement of their breeding strategy. However, the 32-day incubation fast endured by one male prior to abandoning the egg, clearly indicates that birds possess long-term fasting capacity. Excessive rates of mass loss during incubation indicate either that Shy albatrosses are utilizing different fuels than the long-term fasting species, and/or the thermal demands of their environment result in increased evaporative water losses. Birds incubate during Spring/Summer when average daily maximum temperatures are between 14 and 17 ° C. There are behavioural

indications (panting, gaping) that the birds overheat, and this may be manifested physiologically through increased rates of evaporative water loss. Mass loss rates, even after digestion of the stomach contents, were twice that expected on the basis of body mass.

9.5.6 *Continuing threats to Shy albatrosses and future research directions*

The biggest threat facing albatrosses globally remains their incidental by-catch in longline fisheries (Croxall 1998). Within the foraging grounds of adult Shy albatrosses, this threat is represented by the expanding Australian domestic longline fishery targeting tuna. Shy albatrosses are the most frequently caught species in this fishery (Tasmanian Parks & Wildlife Service, unpubl. data), and given both the at-sea distribution of the birds and the current distribution of effort in the fishery, the populations at Pedra Branca and Mewstone are likely to be the most seriously impacted (Chapter 8). While we now understand the distribution of adults during the breeding season, we have little information on either the distribution of adults during the non-breeding period, or on the distribution of juveniles. This knowledge remains deficient for most species and this is of concern as it is often low levels of juvenile recruitment or deaths of adults outside the breeding period that are contributing to the population declines (Gales et al. 1998). Gaining an understanding of the distribution of non-breeding birds must clearly be a priority for future studies. Also, as the status of the Tasmanian populations is known only at Albatross Island, determining both the demographic parameters and trends in population size at Pedra Branca and Mewstone (the two populations most likely to be impacted by longline fisheries within the AFZ), must also be considered as a matter of priority.

The restricted distribution of adult Shy albatrosses and their reliance on a small number of prey species is also an issue of potential concern, given that these prey species are also the targets of commercial fishing operations in Tasmania. There is a large-volume purse-seine fishery for Jack mackerel, which has taken up to 40,000 tonnes of fish per annum since its inception in 1985 (Kailola et al. 1993). There is also a relatively small commercial fishery for Gould's squid (1800 tonnes per year), and most of the squid are taken from the waters of western Bass Strait, within the foraging zone of the Albatross Island population. Given the likely increased importance of squid in the diet of this population during winter, the renewed interest and call for an increase in the Bass Strait squid fishery (McLoughlin et al. 1997, Lister 1998) are cause for considerable concern. Clearly, failure to account for predator requirements and/or overexploitation of either Jack mackerel or Gould's squid would have detrimental impacts upon the Shy albatrosses

breeding in Tasmania.

This study has examined a number of aspects of the foraging ecology of the Shy albatrosses breeding in Tasmania, and it has elevated the species from one of the least known (Croxall 1998) to one of the better understood. It is clear that only armed with a through understanding of albatross ecology coupled with the widespread adoption of appropriate and effective mitigation measures that we can begin to secure a future for albatrosses and succeed in ensuring their long-term survival.

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